May 1946, *P. Allen 3531* (holotype, BH; isotype, MO). Figures 1, 2.

Stems solitary or cespitose, erect, to 12 m tall, 9–18 cm diam. Leaves 6–8; sheaths deciduous, forming a distinct green, maroon, or purple-black crownshaft 68–75 cm long; petiole 20–60 cm long; rachis 1.8–2.5 m long; pinnae 33–51 per side; middle pinnae 118 cm long, 6 cm wide; apical pinna not wider than others. Inflorescence infrafoliar, horizontal; peduncle ca. 20 cm long, 1.8–2.3 cm diam.; prophyll 40–51 cm long, 10.5 cm wide; peduncular bract ca. 1.1 cm long, 4–6 cm wide, inserted 5–6 cm above base of peduncle; rachis 41–85 cm long; rachillae 23–100, to 73 cm long, at anthesis with sessile, crustose, mostly branched hairs (occasionally brown tomentose); flowers glabrous; fruit 10–11 mm diam.; seeds with ruminate endosperm.

Common name. "Maquenque" (Panama).

Distribution. Eastern Nicaragua to western Panama, in cloud forest 1,000–3,000 m.

Additional specimens examined. NICARAGUA. RIVAS: Isla de Ometepe, NW slopes of Volcán Maderas, 11°26–27'N, 85°30–31'W, 1,000–1,350 m, 24 Feb. 1978, *Stevens 6510* (MO). COSTA RICA. ALAJUELA: Reserva Biológica de San Ramón, road from Las Lagunas to Colonía Palmareña, 10°14'N, 84°32'W, 850–1,100 m, 30 May 1986, *de Nevers et al. 7779* (MO). CARTAGO: above Finca La Florita on road from Cartago to El Generál, 2,450 m, 8 Apr. 1953, *Moore 6677* (BH). HEREDIA: Santo Domingo de Vara Blanca, 2,200 m, 22 Feb. 1937, *Valerio 1597* (F). LIMÓN: Cordillera de Talamanca, Atlantic slope, Valle de Silencio, area just N of Cerro Hoffmann, 4.5 airline km W of Costa Rica/Panama border, 9°08'N, 82°58'W, 2,350–2,450 m, *Davidse et al. 28700* (MO). PUNTARENAS: Cerro Echandi, 3,200 m, "Bocas, Panama, Aug. 1983, Musci, epipetric" (sic), *Gómez et al. 21835* (CAS, MO); Monteverde, 10°17'N, 84°47'W, 1,300 m, 7 June 1986, *Hammel 14872* (NY); 1,800 m, 16 June 1986, *Hammel 14960* (NY); between Sabalito and Finca López above Beneficio de Wa Chong, 1 Feb. 1967, *Moore & Parthasarathy 9440* (BH); Las Cruces ridge, San Vito de Java, 1,200 m, 2 Feb. 1967, *Moore & Parthasarathy 9443* (BH). PANAMA. CHIRIQUÍ: 2.2 km SW of Cerro Punta on road above IDAAN water tank, along ridge trail SW of Quebrada Iglesia above vegetable gardens, 2,100–2,250 m, 7 Aug. 1974, *Croat 26316* (MO); Cerro Pate Macho, Pacific side, 2,150 m, 8°49'N, 82°24'W, 31 Dec. 1985, *de Nevers & Charnley 6685* (MO, NY); road to Cerro Punta from Alto Quiel, above Boquete, 3.5 mi. up Cerro Punta road, 1,850 m, 8°51'N, 82°29'W, 16 Jan. 1986, *de Nevers & McPherson 6800* (MO, NY); path above Cerro Punta to Boquete, 8°50'N, 82°30'W, 2,500 m, moist forest, 16 Mar. 1983, *Hamilton & Stockwell 3392* (CAS, MO, NY).

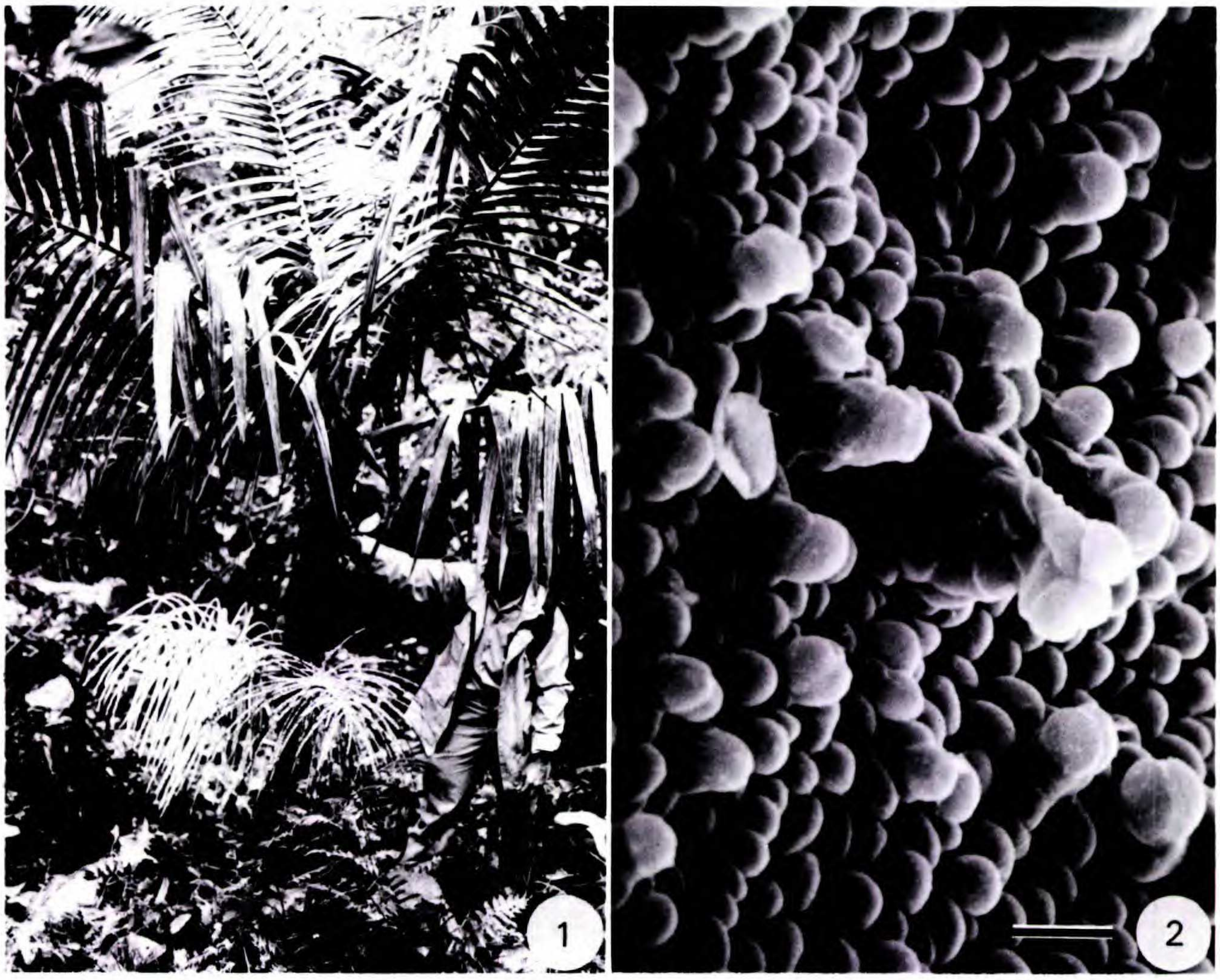
Prestoea allenii varies considerably with altitude. At lower elevations mature plants are sometimes solitary and have green crownshafts, and immature plants can lack crownshafts. At higher elevations the stems are usually cespitose, and the crownshafts maroon or purple-black. In Nicaragua and Costa Rica, lower-elevation populations with green crownshafts may represent a distinct taxon (e.g., *de Nevers et al. 7779*). However, the rachilla hairs are similar to those of *P. allenii*, and such collections are tentatively referred to that species. Robert Read (pers. comm.) reports that color variability in crownshafts of the same species is not uncommon in certain palms.

Prestoea allenii is the largest species of the genus in Central America and occurs at the highest altitude. This is not an uncommon correlation in neotropical palms, occurring, for example, in *Geonoma* and *Chamaedorea*.

2. **Prestoea darienensis** A. J. Henderson, Brittonia 38: 266. 1986. TYPE: Panama. Darién: Serranía de Pirre, on the ridge, 1,130 m, 18 Jan. 1985, *A. Henderson & J. Contraires 97* (holotype, NY; isotype, PMA). Figures 3, 4.

Stem solitary, erect, 2.5 m tall, 10 cm diam. Leaves 6; sheaths persistent, not forming a crownshaft; petiole 80 cm; rachis 165 cm; pinnae 29 per side; middle pinnae 75 cm long, 5 cm wide; apical pinna not wider than others. Inflorescence inter- or infrafoliar, erect; peduncle 75 cm long, ca. 1.5 cm diam.; prophyll 60 cm long, 4 cm wide; peduncular bract 2.23 m long, 2.5 cm wide, inserted 23 cm above base of peduncle; rachis 80–135 cm long; rachillae ca. 60, 45–72 cm long, at anthesis scabrid with crustose, branching hairs; flowers glabrous; fruit 8 mm diam.; seeds with ruminate endosperm.

Distribution. Known only from the type locality.

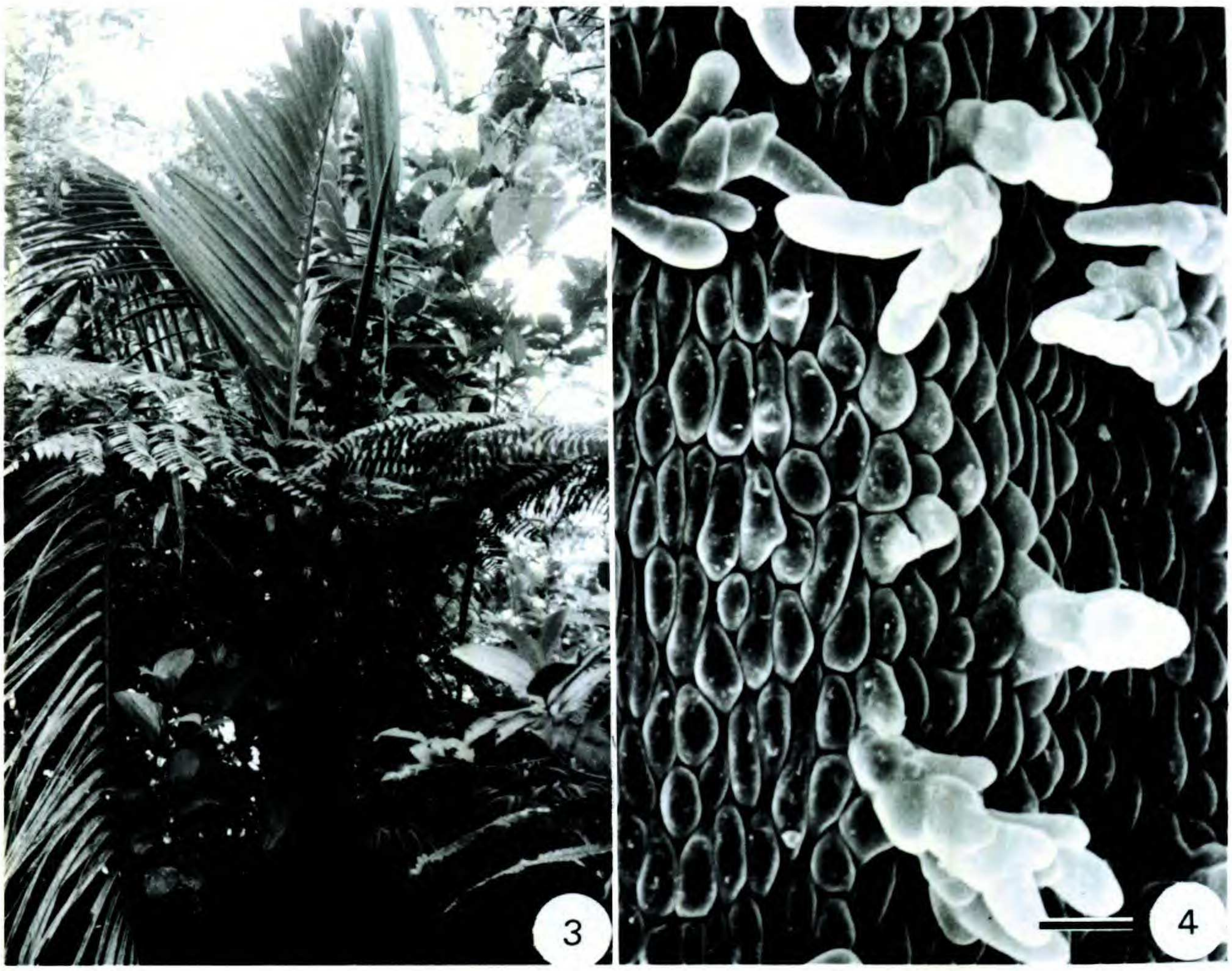


FIGURES 1, 2. Prestoea allenii.—*1. Habit, showing crownshaft and infrafoliar inflorescence (*de Nevers & McPherson 6800*).—2. Part of rachilla, showing sessile, crustose, mostly unbranched hairs (*Allen 3531*). Scale bar = 250 μm.*

Prestoea dariensis can be distinguished from the similar *P. sejuncta* by the rachillae with short, crustose, branching hairs. The inflorescence bud of the type is 2.5 m long, the longest of any *Prestoea* seen, and only approached by some specimens of *P. sejuncta,* which occasionally reach 2.1 m.

3. **Prestoea decurrens** (H. A. Wendl. ex Burret) H. Moore, Gentes Herb. 9: 286. 1963. *Euterpe decurrens* H. A. Wendl. ex Burret, Bot. Jahrb. Syst. 63: 63. 1929. TYPE: Costa Rica. Alajuela: San Carlos, 24 Mar. 1901, *Koschny s.n.* (B, destroyed). Neotype (here designated): Costa Rica. Heredia: Finca La Selva on Río Puerto Viejo just E of its junction with Río Sarapiquí, 12 Dec. 1984, *A. Henderson 50* (NY). Figures 5, 6.

Stems usually cespitose, (1–)2–7, erect, 3–7(–10) m tall, 3.2–10 cm diam., smooth and shiny, green or yellow. Leaves 7–9; sheaths 26–34 cm long, semipersistent, not forming a crownshaft; petiole 50–95 cm long; rachis 1.6–2.3 m long; pinnae 36–50 per side; middle pinnae 52–66 cm long, 3–4 cm wide; apical pinna not wider than the others. Inflorescence infrafoliar, white at anthesis, erect or diagonal; peduncle 15–25(–42) cm long, (0.7–)1–3 cm diam.; prophyll 17.5–19.5 cm long, 3 cm wide; peduncular bract 42–81 cm long, 2.5 cm wide, inserted 2.5–6.5 cm above base of peduncle; rachis 8–27 cm long; rachillae 7–50, 20–56 cm long, at anthesis with short, stiff, simple to branched, white, persistent hairs; staminate petals pilose near apex; fruit 6.5–8 mm diam.; seeds with ruminate endosperm; seedling leaves pinnate.



FIGURES 3, 4. Prestoea darienensis.—*3. Habit, showing long, erect, interfoliar inflorescence bud (*Henderson 97*)*.—*4. Part of rachilla, showing sessile, crustose branching hairs (*Henderson 97*). Scale bar = 250 μm.*

Common name. "Palmitillo" (Costa Rica).

Distribution. Throughout Nicaragua, Costa Rica, and Panama, usually between sea level and 1,500 m. This species is also known from northern Colombia (Galeano-Garcés, 1986).

Additional specimens examined. NICARAGUA. MATAGALPA: Comarca Wanawás, beside Río Bilampi, 12°3′N, 85°13′W, 180–200 m, 14 May 1980, *Moreno & Araquistain 2389* (MO, US). RÍO SAN JUAN: near Caño Chontaleño, 20 km NE of El Castillo (Río Indio watershed), 200 m, 7–9 Mar. 1978, *Neill 3320* (MO); 18 Apr. 1978, *Neill & Vincelli 3495* (MO, US). ZELAYA: "Kurinwacito," 13°8′N, 84°57′W, 80 m, 24 Mar. 1984, *Moreno 23880* (US); Mun. Siuna, Caño El Léon, road to Hormiguero, 2 Feb. 1983, *Ortiz 730* (MO); Mina Nueva America, ca. 11.3 km N of main road leading W from 14.3 km N of El Empalme to Rosita, 22 Apr. 1979, *Pipoly 5322* (US); Caño between Cerro La Pimienta and El Hormiguero, ca. 13°45′N, 85°59′W, 800–1,000 m, 15 Mar. 1980, *Pipoly 6018* (MO, US); ca. 6.3 km S of bridge at Colonía Yolonia and ca. 0.8 km S of ridge of Serranías de Yolonia on road to Colonía Manantiales (Colonía Somoza), 11°36′N, 84°22′W, 200–300 m, 29–31 Oct. 1977, *Stevens 4823* (BH, MO, US); 13–14 Feb. 1978, *Stevens 6387* (MO); Caño Costa Riquita, ca. 1.8 km SW of Colonía Naciones Unidas, above road between Colonía Nueva León and Colonía Naciones Unidas, ca. 11°43′N, 84°18′W, 150–180 m, 6–7 Nov. 1977, *Stevens 5034* (BH, MO, US); S slope of Cerro El Inocente down to near Caño Majagua, ca. 13°45′N, 85°0′W, 800–1,000 m, 9 Mar. 1978, *Stevens 6814* (BH, MO); trail from Cerro Saslaya to San José del Hormiguerro, between Caño Majagua and Caño Sucio, ca. 13°45′N, 84°59′W, 600–800 m, 10 Mar. 1978, *Stevens 6838* (BH, MO); 6.3 km S of bridge of Colonía Yolonia on road to Colonía Manantiales of Nueva Guinea, 200–300 m, 13 Feb. 1978, *Vincelli 250* (MO). COSTA RICA. ALAJUELA: E of San Rafael, S of hot springs, W of La Marina, 10°23′N, 84°23′W, 500 m, 19 May 1968, *Burger & Stolze 5021* (F, NY); plains of San Carlos, 100 m, 3 Apr. 1903, *Cook & Doyle 54* (BH, US); Reserva Biológica de San Ramón, road from Las Lagunas to Colonía Palmareña, 10°4′W, 84°32′N, 850–1,100 m, 30 May 1986, *de Nevers et al. 7780* (MO, NY); slopes of Miravalles, above Bijagua, lower montane rainforest, ca. 1,500 m, Nov. 1982, *Gómez et al. 19185* (CAS, CR, MO); vicinity of Guatuso de San Rafael on Río Frío, 10°43′N, 84°48′W, 80–100 m, 4 Aug. 1949, *Holm & Iltis 996* (BH, MO); Río Cuarto, Sarapiquí valley, 1945, *Langlois 12* (BH); beside Laguna María Aguilar, 780 m, 28 Mar. 1969, *Lent 1531* (NY); 2 km N of

Santa Rosa, 15 km N of Boca Arenal on Quesada–Muelle San Carlos–Los Chiles road, 100 m, 10°38'N, 84°31'W, 28 Apr. 1983, *Liesner et al. 15045* (MO, WIS); Río María Aguilar between Cariblanco and San Miguel, valley of Río Sarapiquí, ca. 700 m, 23 Mar. 1953, *Moore 6560* (BH); between Corazón de Jesús and La Virgen, Río Sarapiquí, 340 m, 24 Mar. 1953, *Moore 6576* (BH); 9.1 km before Venado on road from Arenal, 750 m, 1974, *Read & Daniels 74-26* (US). CARTAGO: between Río Pacuare and Grano de Oro, 7 km below Hacienda Moravia, ca. 900 m, 13 Apr. 1953, *Moore 6699* (BH). HEREDIA: Finca La Selva, on Río Puerto Viejo above junction with Río Sarapiquí, 20 Feb. 1981, *Folsom 9056* (DUKE); 27 June 1979, *Holdridge 5107* (BH); 17 Oct. 1980, *Hammel 10189* (DUKE); 5 May 1982, *Hammel 12036* (DUKE); 10 May 1982, *Hammel 12168* (DUKE); 13 June 1984, *Jacobs 2306* (DUKE); 15 July 1984, *Jacobs & Peralta 2883* (DUKE); 28 Jan. 1967, *Moore & Parthasarathy 9407* (BH); 18 Apr. 1972, *Opler 723* (F); 13 May 1984, *Wilbur & Jacobs 34374* (DUKE); 13 May 1984, *Wilbur & Jacobs 34393* (DUKE); 1 June 1985, *Wilbur 37722* (DUKE). LIMÓN: Hacienda Tapezco-Hda. La Suerte, 29 air km W of Tortuguero, 40 m, 10°30'N, 83°47'W, 7 Mar. 1978, *Davidson et al. 6737* (MO). PUNTARENAS: along short cut road to Golfito from Villa Briceño on Interamerican Highway, W side of Fila Gamba, ca. 6 km from Golfito airport, 8°41'N, 83°12'W, ca. 100 m, 6 Mar. 1985, *Croat & Grayum 59925* (CAS, MO); road to Rincón de Osa, 16.5 km W of Chacarita, 83°22'W, 8°45'N, 25 May 1986, *de Nevers et al. 7755* (MO, NY); along the Camino al Pacifico, W of Rincón de Osa, Osa Peninsula, 30 m, 7 Aug. 1967, *Raven 21593* (DS, F, NY). PANAMA. CHIRIQUÍ: above Chiriquí Grande on road to Fortuna Dam, 20 Jan. 1985, *Read et al. 85-20b* (US). COCLÉ: along river leading up mountain to Alto Calvario and trout stream from La Junta near Limón, 800–1,000 m, 12 Oct. 1977, *Folsom 5904* (BH, MO); forest at base of Cerro Pilón above El Valle, 9 Jan. 1972, *Gentry & Dwyer 3655* (BH, MO); 46 km N from Penonomé on road to Coclesito, 30 m, 22 Feb. 1978, *Hammel 1711* (BH, MO). COLÓN: Río Guanche, 3 km upstream of the road, 27 Oct. 1985, *de Nevers & Charnley 6107* (MO, NY); 18 Jan. 1980, *Moore et al. 10515* (BH); 14 Dec. 1974, *Mori & Kallunki 3716* (BH); 15 Mar. 1986, *Hammel & Trainer 14775* (MO); 6 Oct. 1983, *Nee 7253* (CAS, MO); ridge top leading N from Río Escandaloso toward Cerro Bruja, 450 m, 27 Apr. 1978, *Hammel 2707* (MO). COMARCA DE SAN BLAS: El Llano–Cartí road, km 27.6, Río Pingandi, downstream of road, 9°19'N, 78°55'W, 150 m, 9 Mar. 1985, *de Nevers et al. 5065* (CAS, MO); El Llano–Cartí road, km 26.5, along Río Cartí Chico, 9°19'N, 78°55'W, 200 m, 12 Apr. 1985, *de Nevers et al. 5346* (MO, NY); 13 Mar. 1986, *de Nevers et al. 7379* (MO, NY); Yar Bired, continental divide between Cangandi and San José, 9°20'N, 79°08'W, 400–500 m, 5 Feb. 1986, *de Nevers et al. 6900* (MO, NY); Río Cangandi at confluence of Quebrada Titamibe, 9°24'N, 79°7'W, 60 m, 8 Feb. 1986, *de Nevers & Herrera 7017* (MO, NY); Río Taindi (Taimdi of maps), 2–3 km above confluence with Río Mandinga, 9°25'N, 79°11'W, 3 Apr. 1986, *de Nevers et al. 7626* (MO, NY); 3 Apr. 1986, *de Nevers & Herrera 7629* (MO); trail to Cerro Obu (Habu of maps) from Río Urgandi (Río Sidra), 9°23'W, 78°48'N, 100–300 m, 24 June 1986, *de Nevers & Herrera 7988* (MO); Cerro Mali, near Colombian border, 1,400 m, 23 Jan. 1975, *Gentry & Mori 13823* (BH, MO, NY). PANAMÁ: pipeline road near Gamboa, 9°10'N, 79°45'W, 100 m, 24 Feb. 1985, *de Nevers & Charnley 4942* (MO).

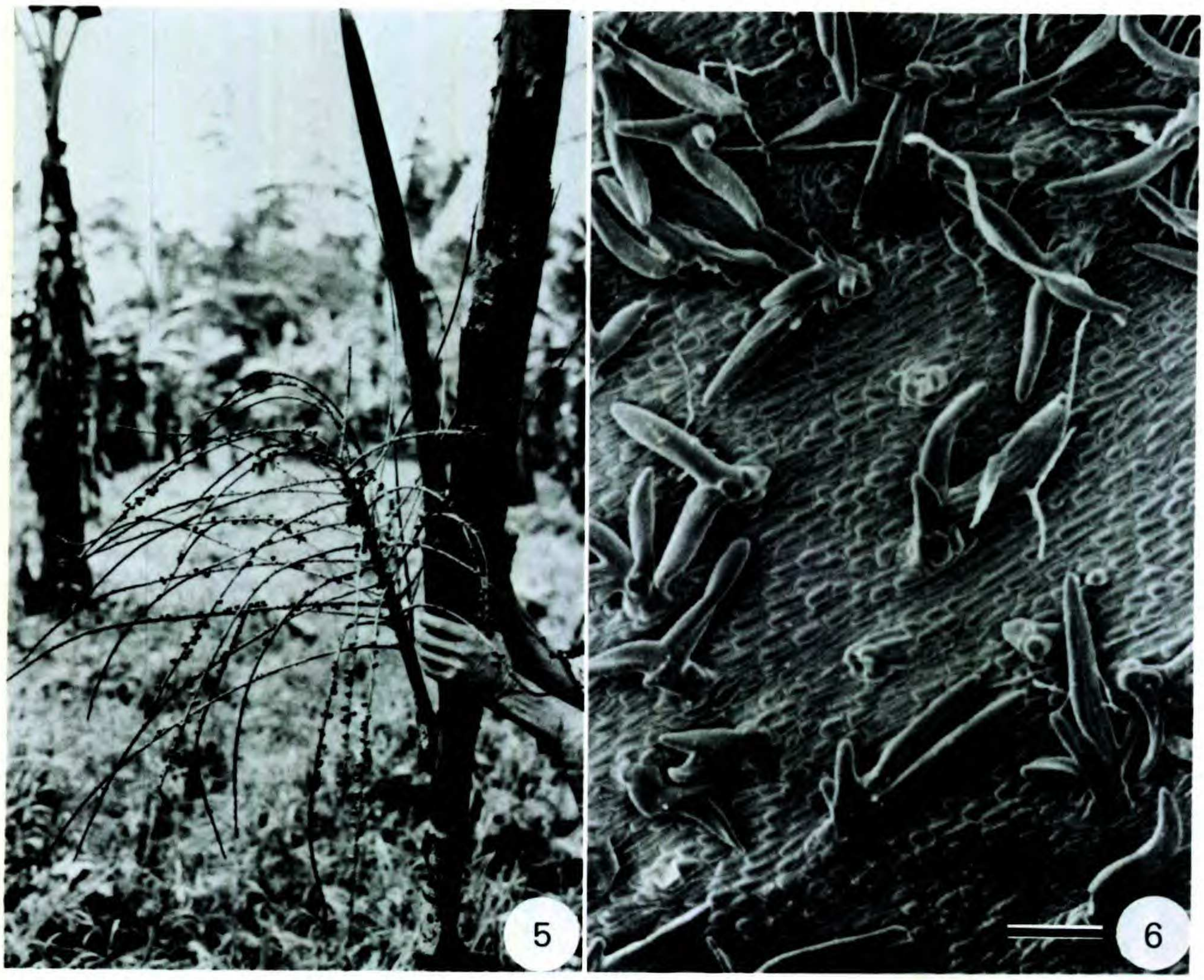
The type is no longer extant at Berlin. Burret cited a paratype (*Wendland 63*) consisting only of fruit. This is not at Göttingen among Wendland's other specimens, and is apparently lost. We therefore designate *Henderson 50*, from the same general area as the paratype, as neotype. Burret (1929) considered *P. decurrens* to be closely related to *Euterpe macrospadix* Oerst. and placed them in the same subsection (see Henderson, 1986), but they are unrelated. The confusion probably arose because the type of *E. macrospadix* at Copenhagen appears to be a mixture of *Prestoea* leaves (probably *P. longipetiolata*) and a *Euterpe* inflorescence.

Specimens from the Osa Peninsula in Costa Rica (*Raven 21593*, *Croat & Grayum 59925*) and Río Guanche in Panama have the typical tomentum of *P. decurrens*, but the inflorescence is less stout, the peduncle is longer and thinner, and there are 7–20 (vs. 50) rachillae. The strongly cespitose (vs. erect) stems are thinner and weaker than usual for the species.

4. **Prestoea integrifolia** de Nevers & A. J. Henderson, sp. nov. TYPE: Panama. Colón: Santa Rita Ridge, km 21.2, 9°20'N, 79°45'W, 350 m, 24 Feb. 1986, *G. de Nevers 7212* (holotype, MO; isotypes, CAS, COL, K, PMA, NY). Figures 7, 8.

Ab aliis speciebus integrifolius inflorescentia erecta, rachillis tenuibus pilis simplicibus obsitis necnon seminum endospermate ruminato diversa.

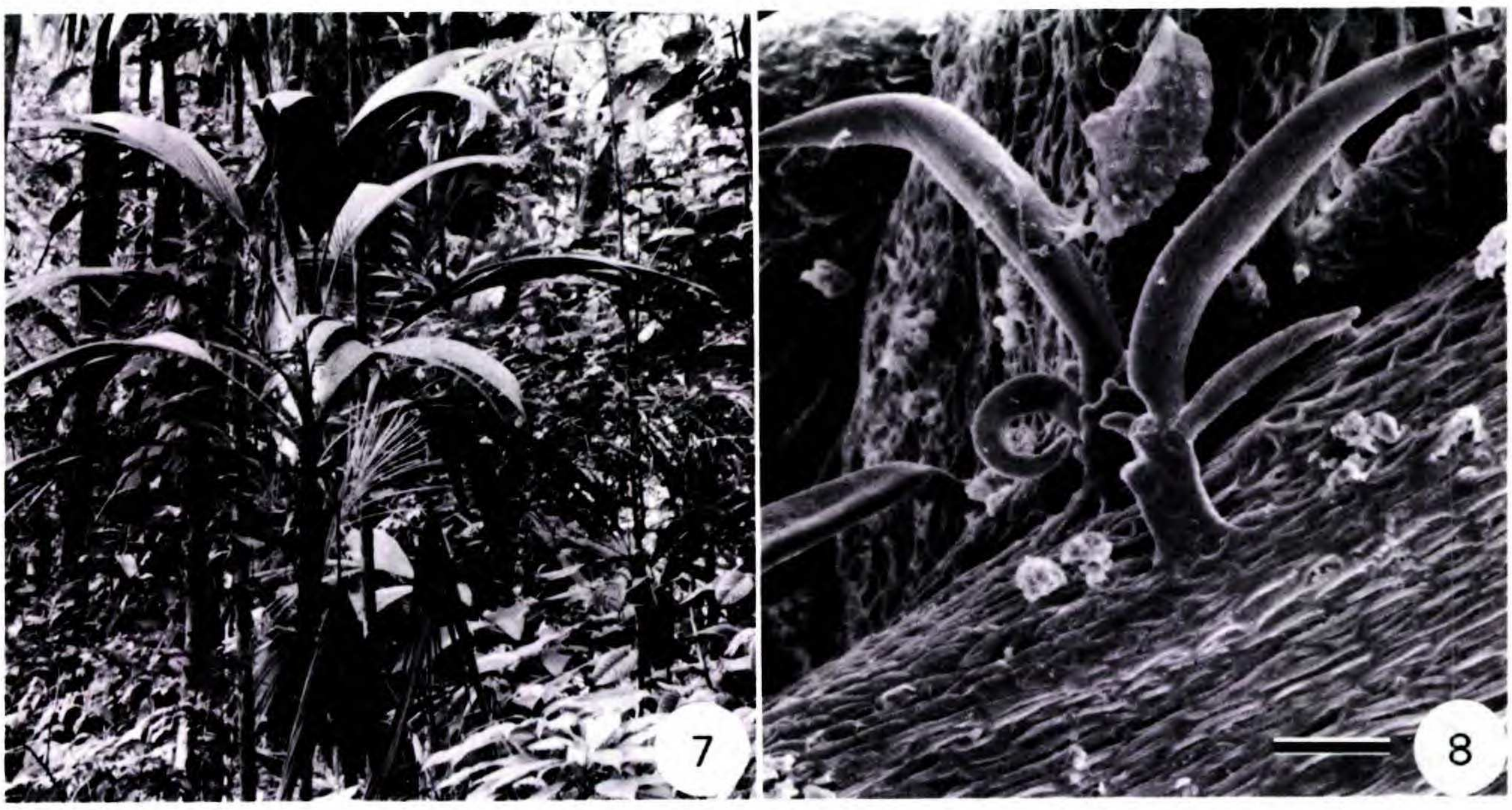
Stems cespitose, one well-developed, erect, 2.8–5.8 m tall, 3–4 cm diam.; internodes 3–8 cm long; adventitious roots forming a prominent cone at base of stem, 18–30 cm long, 6–8 mm diam., red, covered with small round projections. Leaves 8–12, spreading; sheaths not forming a crownshaft, 30–38 cm long, closed basally for 15–18 cm, open apically, covered sparsely with closely appressed whit-



FIGURES 5, 6. Prestoea decurrens.—*5. Habit, showing smooth stem, persistent leaf sheaths not forming a crownshaft, erect, interfoliar inflorescence bud, and infrafoliar inflorescence* (Langlois 12). *Photograph courtesy of BH.—6. Part of rachilla, showing short, stiff, simple to branched hairs* (Henderson 50). *Scale bar = 500 µm.*

ish-brown scales; petiole channeled adaxially, rounded abaxially, 30–50 cm long, covered with closely appressed brown scales; rachis 40–65 cm long, ridged adaxially, rounded abaxially and with scales similar to those of petiole; blade entire, 103–113 cm long, 30–35 cm wide, deeply bifid at apex for 60–65 cm; veins prominent adaxially, 14–15 per side, with brown scales proximally. Inflorescence interfoliar, erect at anthesis; peduncle 40–75 cm long, sparsely covered with brown scales; prophyll 21–35 cm long, covered with scales similar to those of peduncle; peduncular bract inserted 5–10 cm above base of peduncle, 80–130 cm long, with scales similar to those of peduncle, at anthesis brown on outside, whitish on inside; rachis 18–32 cm long; rachillae 23–28, 35–54 cm long, 1 mm diam. at middle at anthesis; rachis and rachillae white at anthesis, becoming reddish in fruit, with sparse, hyaline, simple or branched hairs; triads subtended by a low bract; staminate flowers 4 mm long, sessile; sepals 3, free, imbricate, triangular, keeled, membranaceous, hyaline margined, apiculate, 1.5 mm long; petals 3, free, valvate, lanceolate, 4 mm high; stamens 6; filaments unequal, 0.9–1.5 mm long; anthers dorsifixed at center of thecae, introrse; thecae unequal, 0.8–1.2 cm long; pistillode 1 mm long, deeply trifid; pistillate flowers 2 mm long, surrounded by 2 low bracteoles; sepals 3, free, imbricate, glabrous, broadly ovate; petals similar to sepals but slightly smaller; gynoecium ovoid, pseudomonomerous, 1.5 mm long; stigmas sessile; staminodes minute, dentate; immature fruits with ruminate endosperm.

Distribution. Only known from the type locality.



FIGURES 7, 8. Prestoea integrifolia.—*7. Habit, showing entire leaves and interfoliar, erect inflorescence (*de Nevers 7212*).—8. Part of rachilla, showing hyaline, simple and branched hairs (*de Nevers 7212*). Scale bar = 500 μm.*

Additional specimens examined. PANAMA. COLÓN: same locality as type, 13 May 1986, *de Nevers et al. 7738* (MO, NY); km 22, 500 m, 17 Feb. 1986, *Hammel et al. 14473* (MO, NY).

Prestoea integrifolia differs from all other Central American members of the genus by its entire leaves. Three other extra-Central American species have entire leaves: *P. simplicifrons*,[4] *P. simplicifolia* Galeano, and *P. cuatrecasasii* H. Moore.

The holotype of *P. simplicifrons* is no longer extant at B, and no isotypes are known, but there is another collection from at or near the type locality (*Henderson & Bernal 156*). Thus represented, *P. simplicifrons* has relatively short rachillae with a moderate to dense covering of reddish brown hairs, whereas *P. integrifolia* has long rachillae sparsely covered with hyaline hairs.

Prestoea simplicifolia (represented at NY by an isotype and by *Henderson & Bernal 140*) has a stout, pendulous inflorescence with thick rachillae, in contrast with *P. integrifolia,* which has a thin, erect inflorescence with thin rachillae.

Prestoea cuatrecasasii (represented by the original description) has seeds with homogenous endosperm, as opposed to the ruminate endosperm of *P. integrifolia.*

Prestoea pubigera (Griseb. & H. A. Wendl.) Hook. f. is sometimes reported to have entire leaves (e.g., Galeano-Garcés, 1986), but all specimens examined, including the type at Göttingen, have the lower part of the leaf with separate but unequal pinnae, and these are joined in the upper part.

5. **Prestoea longipetiolata** (Oersted) H. Moore, Gentes Herb. 9: 286. 1963. *Euterpe longipetiolata* Oerst., Vidensk. Meddelel. Kjoebenh. 1858: 32. 1859. TYPE: Costa Rica. Cartago: Turrialba, May 1847, *A. S. Oersted 6562* (holotype, C). Figures 9, 10.

Euterpe brachyspatha Burret, Bot. Jahrb. Syst. 63: 57. 1929. TYPE: Costa Rica. Puntarenas: Cañas Gordas, 1,100 m, Feb. 1897, *H. Pittier 11124* (holotype, B destroyed; isotypes, M, US).

Euterpe williamsii Glassman, Fieldiana, Bot. 31: 5. 1964. TYPE: Nicaragua. Matagalpa: Cordillera Central de Nicaragua, along road to La Fundadora, cloud forest area, 1,300–1,400 m, 23 Feb. 1963, *L. O. Williams, A. Molina & T. P. Williams 24922* (holotype, F).

Malortiea simiarum Standley & L. O. Williams, Ceiba 3: 102. 1952. *Euterpe simiarum* (Standley & L.

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[4] **Prestoea simplicifrons** (Burret) A. J. Henderson & de Nevers, comb. nov. *Euterpe simplicifrons* Burret, Engler Bot. Jahrb. 63: 53. 1929.

O. Williams) H. Moore, Principes 1: 145. 1957. TYPE: Nicaragua. Jinotega: vicinity of Finca San Roque, sierra E of Jinotega, 1,300–1,500 m, 5 July 1947, *P. Standley 10923* (holotype, F).

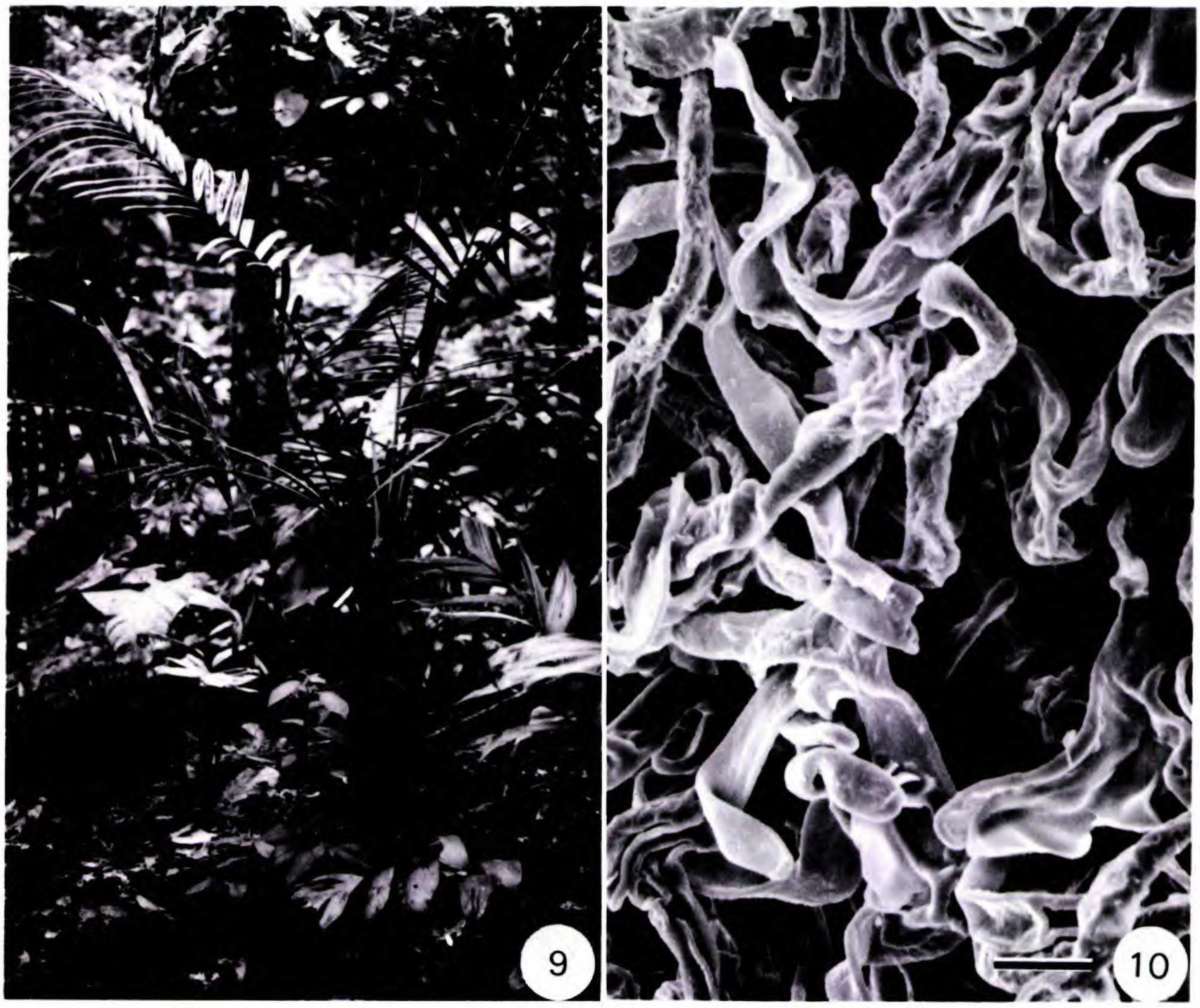
Stems solitary or cespitose, often procumbent, 0.5–3 m tall, ca. 5 cm diam. Leaves 4–8; sheaths persistent, not forming a crownshaft; petiole 80–240 cm long; rachis 116–209 cm long; pinnae 21–33 per side; middle pinnae 45–56 cm long, 1.5–3 cm wide; apical pinna often markedly wider than others. Inflorescence interfoliar or infrafoliar, arching; peduncle 12–100 cm long, 3–6(–11) mm diam.; prophyll (9.5–)15–30 cm long, 1.5–2 cm wide; peduncular bract (32–)56–114 cm long, 2–4 cm wide; rachis 2–9 cm long; rachillae (2–)3–8(–20), (8–)16–35 cm long, at anthesis densely reddish brown tomentose; flowers glabrous; fruit 6–11 mm diam.; seeds with ruminate endosperm.

Distribution. From Nicaragua to western Panama (Chiriquí), 1,000–1,800 m. Contrary to a report by Wessels Boer (1971), this species does not occur in Venezuela (Henderson & Steyermark, 1986).

Additional specimens examined. Nicaragua. JINOTEGA: Ocotillo near Sta. Lastenia, Cordillera Centrál de Nicaragua, 1,550 m, 17 Jan. 1965, *Williams et al. 27806* (F, NY). MATAGALPA: Cerro Carlota, 12°58′N, 85°52′W, 1,250–1,300 m, 23 Oct. 1982, *Moreno 18129* (MO); Cerro El Picacho, N of Selva Negra, 13°0′N, 85°55′W, 1,500 m, 7 July 1983, *Moreno 21670* (MO, US); 7 July 1983, *Moreno 21671* (MO); Cerro Carlota, 12°58′N, 85°52′W, 1,250–1,300 m, *Moreno 18149* (MO); along Highway 3, ca. 1.9 km W of Aranjuez road entrance, ca. 13°2′N, 85°56′W, 1,460–1,480 m, 30 June 1983, *Stevens 9168* (MO, US); along Highway 3, ca. 1 km NW of La Fundadora entrance, unnamed peak ca. 500 m W of Highway, ca. 13°1′N, 85°56′W, 1,450–1,520 m, 24 May 1981, *Stevens & Henrich 20456* (MO); W slope of summit of Cerro El Picacho, ca. 13°0′N, 85°55′W, 1,350–1,590 m, 3 June 1983, *Stevens & Moreno 22168* (MO, US); Cordillera Central de Nicaragua, along road to La Fundadora, 1,300–1,400 m, 23 Feb. 1963, *Williams et al. 24918* (F); Cordillera Central de Nicaragua, Xelaju, 13°02′N, 85°55′W, 1,500 m, 12 Feb. 1965, *Williams et al. 29266* (F, NY). Costa Rica. ALAJUELA: Buena Vista, road to San Carlos valley, 600 m, 11 Apr. 1903, *Cook & Doyle 38* (US); Juan Viñas, Reventazón valley, near Juan Viñas River, 1,000 m, 21 Apr. 1903, *Cook & Doyle 173* (US); along Camino Raíz de Hule, SE of Planatillo (Tsipiri), 1,200–1,400 m, 1 July 1976, *Croat 36792* (MO); Reserva Biológia de San Ramón, road from Las Lagunas to Colonía Palmareña, 10°4′N, 84°22′W, 850–1,100 m, 30 May 1986, *de Nevers et al. 7769* (MO, NY); near Río Naranjo, 2 km W of Orosi, 1,400 m, 16 Jan. 1977, *Lent 4066* (F); slopes of ridge separating Río Paz Grande and Río Paz Chiquita, about halfway between Vara Blanca and Cariblanco, valley of Río Sarapiquí, 1,340–1,500 m, *Moore 6639* (BH); Paraiso, area of Muñeco, 9–10 Mar. 1974, *Read & Daniels 74-80* (US); Guadalupe de Zarcero, 1,200 m, 1 Nov. 1973, *Smith A567* (F); La Peña de Zarcero, Cantón Alfar Ruiz, 1,375 m, 23 Jan. 1939, *Smith 1544* (NY); El Muñeco, S of Navarro, 1,400 m, 8 Feb. 1924, *Standley 33600* (F, US). CARTAGO: Cañón del Río Grande de Orosi y Aluvión, 23 Oct. 1983, *Chacon et al. 1489* (MO); Río Tambor, 3 km SE of Cachí, 1,420 m, 22 Aug. 1971, *Lent 2060* (F); about 5 km beyond Hacienda Moravia, 1,000–1,200 m, 13 Apr. 1953, *Moore 6686* (BH); fords of Las Vueltas, Tucurrique, 635 m, Dec. 1898, *Tonduz 12924* (F, US). PUNTARENAS: Finca Loma Linda, 1 mi. SW of Cañas Gordas, 1,150 m, 26–27 Feb. 1973, *Croat 22232* (CAS, K, MO); foothills of the Cordillera de Talamanca, around Tres Colinas, 9°07′N, 83°04′W, 1,800–1,850 m, 20 Mar. 1984, *Davidse et al. 25609* (MO); Monteverde, along Río Guacimal below Lechería, 10°17′N, 84°48′W, 1,500 m, 11–14 June 1985, *Hammel & Trainer 13822* (CAS, MO); 16 June 1985, *Hammel 13872* (MO); Monteverde area, valley of Río San Luis just S of Monteverde, 10°16′N, 84°48′W, 1,000–1,200 m, 18 June 1985, *Hammel & Haber 13924* (MO); 1,800 m, 16 June 1986, *Hammel 14961* (NY); Finca Las Cruces, on trail to Río Java, ca. 1,000 m, 31 Jan. 1967, *Moore & Parthasarathy 9426* (BH); Monteverde, along foot trail in forest reserve, 3 Nov. 1974, *Moore et al. 10170* (BH); Las Cruces, Finca Kilpauk, 15 Dec. 1961, *Read 655* (BH); San Vito de Coto Brus, Las Cruces Botanical Garden, Jan. 1985, *Wilson s.n.* (BH). SAN JOSÉ: El General, 1,490 m, Feb. 1939, *Skutch 4184* (US); between San Isidro and La Georgina, 17 Nov. 1973, *Moore & McAlpin 10150* (BH); 17 Nov. 1973, *Moore & McAlpin 10150A* (BH). Panama. BOCAS DEL TORO: La Fortuna Dam Area, N of dam along continental divide trail W of oleoducto road, 8°47′N, 82°15′W, 1,200–1,300 m, 11 Feb. 1986, *Hammel & McPherson 14458*; near continental divide in vicinity of Cerro Colorado, 9.4 road miles from Chami camp, ca. 8°35′N, 81°45′W, ca. 1,700 m, 15 Apr. 1986, *McPherson 8917* (MO, NY). CHIRIQUÍ: 9 mi. from Río Chiriquí Viejo bridge near Nueva California on road to Río Sereno, 7 Apr. 1979, *Hammel et al. 6829* (MO).

Malortiea simiarum was originally distinguished by its pinnate leaves and little-branched inflorescence when being compared with *Reinhardtia* (*Malortiea*). The size, degree of branching, and pubescence of the type fall within the range of variation observed in Costa Rican material of *P. longipetiolata*.

Euterpe brachyspatha, as judged from the original description, was named after a misinterpretation of the inflorescence. Burret (1929) described the spadix (inflorescence) as 98 cm long and the spathe (peduncular bract) as 17 cm long, which is impossible. The ho-



FIGURES 9, 10. Prestoea longipetiolata.—*9. Habit, showing procumbent stem and arching, interfoliar inflorescence (*Moore 9426*). Photograph courtesy of BH.—10. Part of rachilla, showing dense tomentum (*McPherson 8917*). Scale bar = 250 µm.*

lotype is lost, and the isotypes are incomplete. However, the specimens described by Burret represent *P. longipetiolata*. The Munich isotype has the broad apical pinna typical of most but not all specimens of *P. longipetiolata*. A topotype, *Croat 22232*, is typical *P. longipetiolata*.

Euterpe williamsii was originally contrasted with *E. brachyspatha*, presumably represented by the original description. In Burret's (1929) key, *E. brachyspatha* and *E. longipetiolata* are contrasted in the same couplet. In its protologue, Glassman did not contrast *E. williamsii* with *E. longipetiolata*. *Euterpe williamsii* agrees in the diagnostic characters of size, branching, and pubescence of the inflorescence with *E. longipetiolata*.

6. Prestoea roseospadix (L. Bailey) H. Moore, Principes 9: 73. 1965. *Euterpe roseospadix* L. Bailey, Gentes Herb. 6: 201. 1943. TYPE: Panama. Chiriquí: vicinity of Bajo Chorro, 1,900 m, 20–22 July 1940, *R. E. Woodson & R. W. Schery 623* (holotype, MO; isotype, BH). Figure 11.

Stems solitary, erect, 0.3–3 m tall, 8–10 cm diam. Leaves 4–6; sheaths persistent, not forming a crownshaft; petiole 61–76 cm long; rachis 120–125 cm long; pinnae 21–27 per side; middle pinnae 38–50 cm long, 2–2.5 cm wide; apical pinna not wider than others. Inflorescence infrafoliar, erect; peduncle 16–38 cm long, 0.5 cm wide; prophyll 20–23 cm long, 2 cm wide; peduncular bract 70–80 cm long, 2 cm wide, inserted ca. 14 cm above base of peduncle; rachis 16–40 cm long; rachillae 9–16, 20–40 cm long, glabrous; flowers glabrous; fruit 9–10 mm diam.; seeds with ruminate endosperm.

Distribution. Western Panama (Chiriquí and Veraguas) at altitudes around 1,500 m.

Additional specimens examined PANAMA. CHIRIQUÍ: Cerro Horqueta, 2,100 m, 24 July 1966, *Blum & Dwyer 2665* (MO); 24 July 1966, *Blum & Dwyer 2671* (MO); 8 Aug. 1967, *Kirkbride 162* (MO); Bajo Chorro, Boquete, ca. 2,000 m, 11 Jan. 1938, *Davidson 100* (F); lower slopes of Cerro Pate Macho, 8°49'N, 82°24'W, 1,600 m, 31 Dec. 1985, *de Nevers & Charnley 6697* (MO, NY); 17 Jan. 1986, *de Nevers & McPherson 6829* (MO, NY); La Fortuna hydroelectric dam project, behind camp, 1,300–1,400 m, 23 Mar. 1978, *Hammel 2255* (BH, MO). VERAGUAS: valley of Río Dos Bocas on road between Alto Piedra (above Santa Fé) and Calovébora, 350–400 m, 29 Aug. 1974, *Croat 27440* (MO).

7. **Prestoea sejuncta** L. Bailey, Gentes Herb. 6: 201. 1943. TYPE: Panama. Canal Area: Madden Lake area, upper Río Pequení, 100 m, 29 July 1941, *A. G. B. Fairchild & D. Jobbins 2635* (holotype, BH; isotype, MO). Figures 12–14.

Stem solitary or cespitose, erect, 5–9 m tall, (4.5–)9–13 cm diam. Leaves 5–8; leaf sheaths persistent or deciduous, not forming a crownshaft; middle pinnae 61–86 cm long, 3–4.5(–6) cm wide; apical pinna not wider than others. Inflorescence interfoliar, erect, or arching, or horizontal, straight or curved; prophyll 13–45(–75) cm long, (1.2–)3–5 cm wide; peduncular bract 69–156(–215) cm long, (2.5–)3.6–5.5 cm wide, inserted (2–)4.5–13 cm above prophyll; peduncle 23–71 cm long, 0.6–1.4 cm wide, narrow, cylindric, not flaring at base; rachis (15–)33–50 cm long; rachillae (18–)42–48, 30–70 cm long, essentially glabrous but with patches of long, loosely intertwined hairs; flowers glabrous; fruits 7–10 mm diam.; seeds with ruminate endosperm.

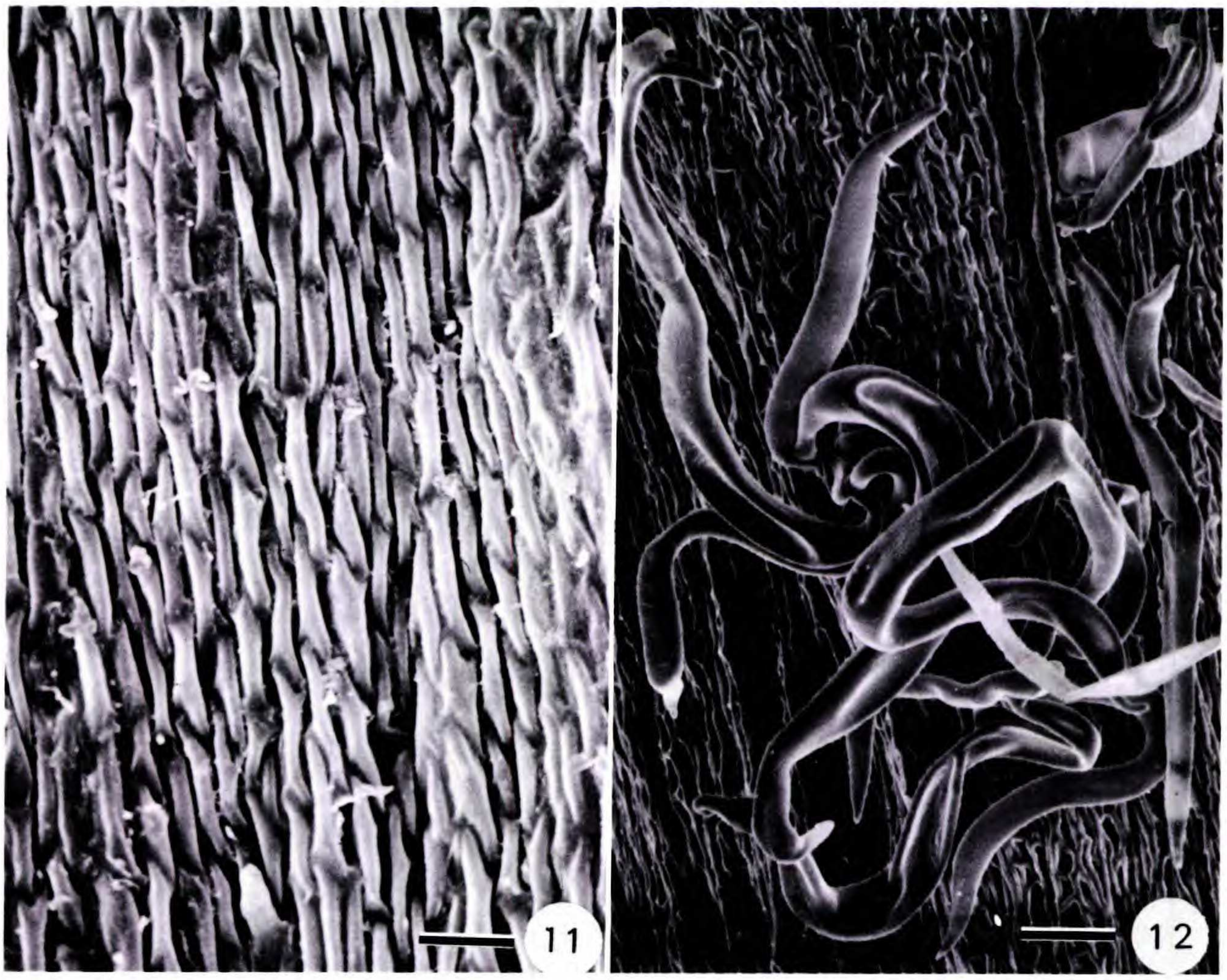
Distribution. Known from central Panama (Chiriquí, Coclé, Comarca de San Blas, Colón), 100–1,100 m. This species is also reported from coastal Ecuador by Dodson & Gentry (1978). Other specimens from Ecuador (e.g., *Balslev & Henderson 62107*) are clearly referable to this species, and it presumably occurs in intervening Colombia.

Additional specimens examined. PANAMA. CHIRIQUÍ: Fortuna dam area, road from Gualaca to Chiriquí Grande, continental divide trail west of road, 1,150 m, 8°45'N, 82°15'W, 18 Jan. 1986, *de Nevers & McPherson 6849* (MO, NY). COLÓN: trail from Alto Pacora to Cerro Brewster, 9°18'N, 79°16'W, 700 m, 18 Nov. 1985, *de Nevers et al. 6223* (MO, NY). COCLÉ: El Valle de Antón, La Mesa, ca. 1,000 m, 2 Sep. 1941, *Allen 2740* (paratype) (BH, MO). COMARCA DE SAN BLAS: Cerro Brewster, 9°18'N, 79°16'W, 850 m, 25 Apr. 1985, *de Nevers et al. 5541* (MO, NY). PANAMÁ: 3 mi. N of Cerro Azúl, 26 July 1970, *Croat 11589* (MO); Cerro Jefe, ca. 700 m, 20 Jan. 1980, *Moore et al. 10522* (BH); Río Pequení, slopes of Cerro San Francisco, 150–300 m, 9°22'N, 79°31'W, 29 Nov. 1985, *de Nevers & Henderson 6411* (CAS, MO, NY); road to Alto Pacora from Cerro Jefe, 700 m, 28 Nov. 1985, *Henderson & Brako 505* (MO, NY); Gorgas Memorial Lab's yellow fever research camp, ca. 25 km NE of Cerro Azúl on Río Piedras, 550 m, 20–22 Nov. 1974, *Mori & Kallunki 3454* (BH, MO).

Among the specimens examined, there appear to be two ecotypes, which may turn out to represent distinct taxa. At higher altitudes (900–1,200 m) in premontane rain forest (Holdridge et al., 1971), the inflorescence is straight and erect in bud (Fig. 13) and relatively long and thick (1.5–2.1 m × 3–5 cm). At lower altitudes (10–200 m) in tropical moist forest and tropical wet forest (Holdridge et al., 1971), the inflorescence is curved and horizontal in bud (Fig. 14) and is relatively short and thin (75–80 × 1.2–2.5 cm). When Bailey described *P. sejuncta,* he cited two specimens, one of each ecotype. The holotype is the short-inflorescence ecotype, and the paratype, *Allen 2740,* is the long-inflorescence ecotype. Although letters accompanying *Allen 2740* from Paul Allen to Bailey clearly outlined this variation, Bailey included only the dimensions of the smaller Madden Lake plant.

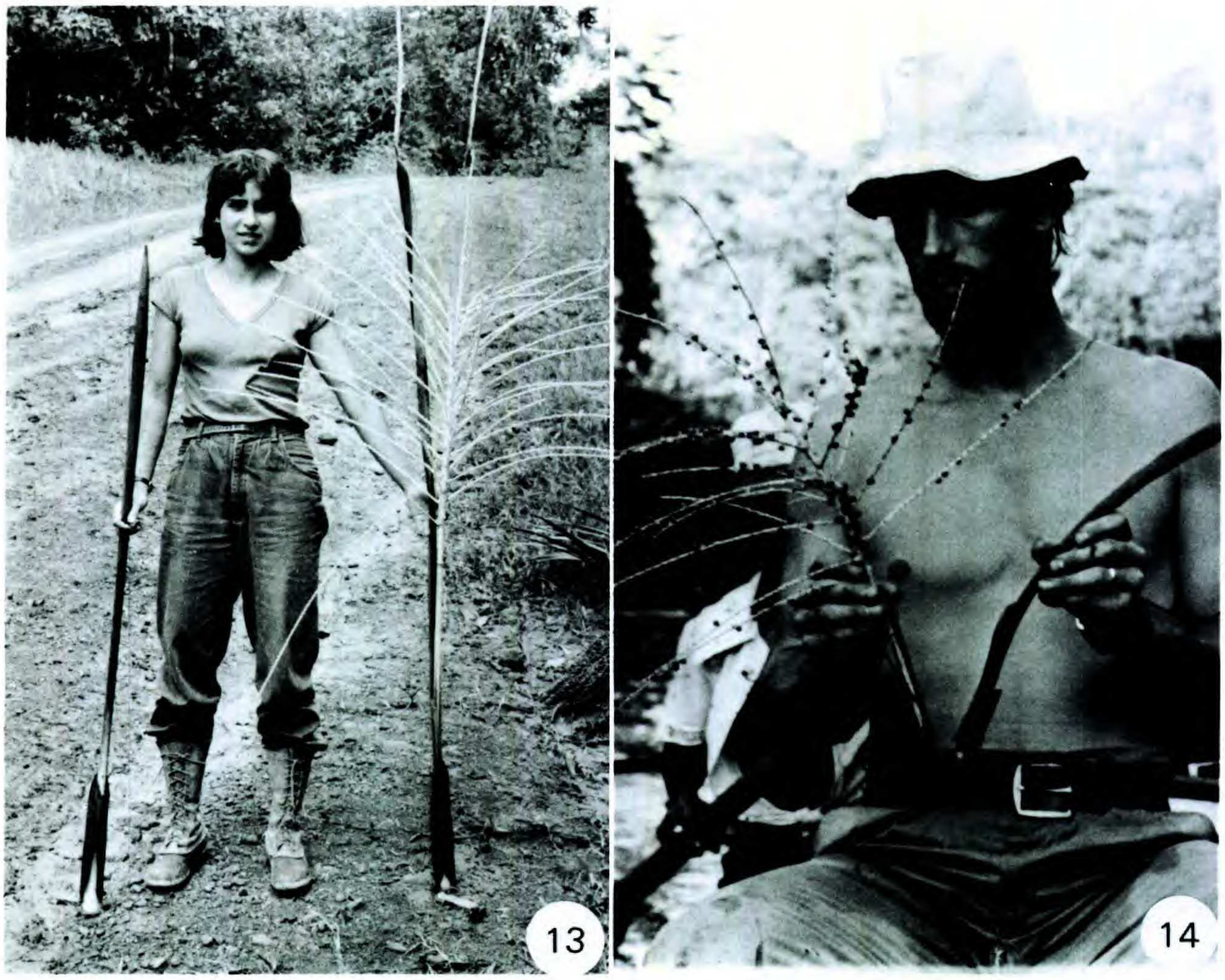
8. **Prestoea semispicata** de Nevers & A. J. Henderson, sp. nov. TYPE: Panama. Comarca de San Blas: Cerro Brewster, 9°18'N, 79°16'W, 800 m, premontane rain forest, 19 Nov. 1985, *G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6290* (holotype, MO; isotypes, AAU, BH, CAS, COL, FTG, K, NY, PMA). Figures 15, 16.

Ab omnibus congeneribus inflorescentia simplice vel pauciramosa necnon seminum endospermate subruminato diversa.



FIGURES 11, 12. Prestoea.—*11.* P. roseospadix, *part of rachilla, showing absence of hairs (*Woodson 623*). Scale bar = 400 μm.—12.* P. sejuncta, *part of rachilla, showing long, loosely intertwined hairs (*de Nevers & Henderson 6411*). Scale bar = 500 μm.*

Stems cespitose, only one well-developed, to 145 cm long, 3.5–9 cm diam., often procumbent and partly subterranean; roots visible above ground, spiny and occasionally swollen. Leaves 4–10, arching to erect; sheaths not forming a crownshaft, 17–20 cm long, brown, persistent; petiole 29–100 cm long, densely covered with closely appressed, brown hairs; rachis 52–180 cm long; pinnae 12–20 per side, elliptic, abruptly and asymmetrically long-apiculate, glossy green adaxially, lighter green abaxially; middle pinnae 19–51 × 2.5–6 cm. Inflorescence infrafoliar, protandrous, arching, borne at or near ground level; peduncle 6–50 cm long, 1.5–3 mm diam., terete, with scattered brown scales; prophyll erect and persistent in leaf axil, inserted at base of peduncle, (1.2–)4.5–19 cm long, 1.1–1.8 cm wide, dorsiventrally compressed, ancipitous, splitting apically; peduncular bract (9–)29–90 cm long, 1–2 cm wide at middle, inserted (0.7–)1.5–7 cm above insertion of prophyll, terete in bud, apically pointed, brown at anthesis, soon dropping; rachillae 1(–4), 8–30 cm long, glabrous; peduncle and rachis white at anthesis and becoming red in fruit; triads densely crowded and borne to apex of rachillae, slightly sunken, subtended by a low bract; staminate flowers 4 mm long, sessile or borne on a short, flattened pedicel, white; sepals 3, triangular, gibbous, imbricate below, 1 mm long, ciliate; petals 3, free, lanceolate, valvate, 4 mm long; stamens 6; filaments slightly flattened, with long reflexed apex in bud, 3 mm long; anthers dorsifixed, latrorse, 2 mm long; pistillode prominent, as long as stamens in bud, briefly trifid at apex; pistillate flower 3 mm long, surrounded by 2 low bracteoles; sepals 3, free, imbricate, minutely ciliate; petals 3, free, val-



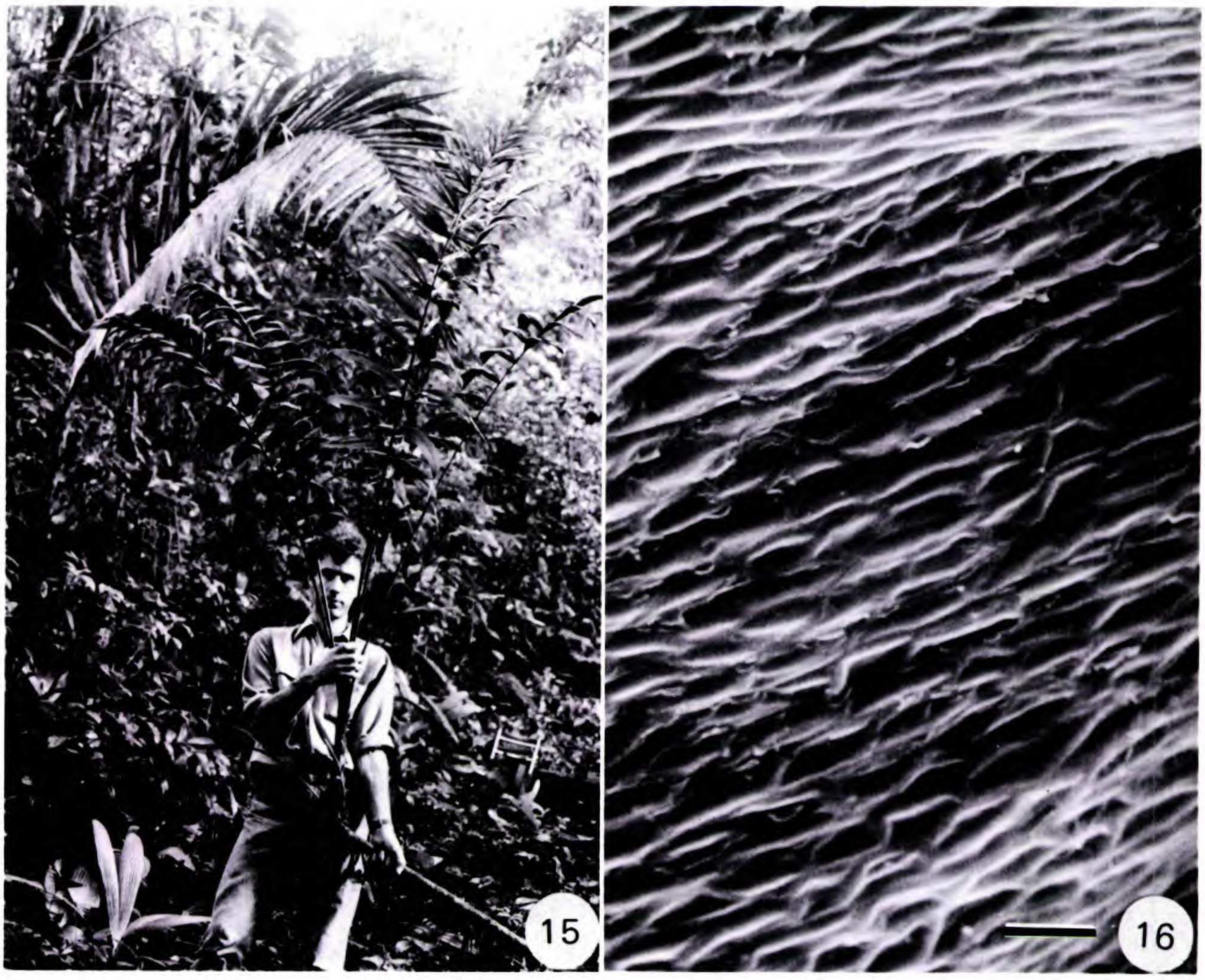
FIGURES 13, 14. Prestoea sejuncta.—*12. Straight inflorescence bud and long inflorescence with elongate peduncle and numerous rachillae (*Henderson & Brako 505*).—14. Curved inflorescence bud and small inflorescence with short peduncle and few rachillae (*de Nevers & Henderson 6411*).*

vate above, imbricate below; gynoecium ovoid, pseudomonomerous, 2 mm long, the ovule attached laterally; stigmas sessile, elongate, not recurved at anthesis; staminodes dentiform; fruit spherical, 8 mm diam., with lateral stigmatic residue, black; epicarp smooth; mesocarp fleshy; seed spherical, 7 mm diam., the endosperm homogenous to slightly ruminate; embryo basal.

Common name. "Siler burwi" (Kuna, Panama).

Distribution. Known only from the low mountains of Central Panama, from the western end of the Serranía de San Blas to El Copé in Coclé, where it is uncommon between 350 and 850 m. It grows on steep slopes and ridge tops in premontane rainforest and tropical wet forest.

Additional specimens examined. PANAMA. COCLÉ: El Valle de Antón, Cerro Gaital, 8°37'N, 80°6'W, 1,000 m, 26 Nov. 1985, *de Nevers et al. 6351* (CAS, MO, NY); continental divide above El Copé, 900 m, 19 Jan. 1978, *Hammel 967* (MO); 27 Nov. 1985, *de Nevers et al. 6381* (MO, NY, PMA, other duplicates to be distributed). COMARCA DE SAN BLAS: same locality as type, 16 Oct. 1984, *de Nevers et al. 4027* (MO, NY); 25 Apr. 1985, *de Nevers et al. 5550* (MO, NY); 19 Nov. 1985, *de Nevers et al. 6242* (MO, NY); 21 Dec. 1985, *Hammel & de Nevers 13560* (CAS, MO); El Llano–Cartí road, km 16.5, 9°19'N, 78°55'W, 350 m, 13 Mar. 1985, *de Nevers & Herrera 5153* (MO); 12 Mar. 1986, *de Nevers et al. 7371* (MO); 22 Nov. 1985, *de Nevers & Henderson 6312* (MO, NY); 8 Mar. 1986, *de Nevers & Herrera 7260* (MO, NY); 18 June 1986, *de Nevers & Herrera 7945* (CAS, MO); trail from Cerro Camucañala to Río Titamibe, 9°24'N, 79°8'W, 60–100 m, 28 Jan. 1985, *de Nevers et al. 4719* (CAS, MO, NY); trail from Río Esadi to Cerro Banega, 300–530 m, 9°23'N, 78°51'W, 21 Dec. 1985, *de Nevers & Herrera 6671* (CAS, MO, NY); Yar Bired (Cerro San José), continental divide between Cangandi and San José, 9°20'N, 79°8'W, 400–500 m, 7 Feb. 1986, *de Nevers & Herrera 6961* (MO, NY); trail to Cerro Obu (Habu of maps) from Río Urgandi (Río Sidra), 9°25'N, 79°11'W, 100–300 m, 3 Apr. 1986,



FIGURES 15, 16. Prestoea semispicata.—*15. Habit, showing procumbent stem, arching, infrafoliar inflorescence, and abruptly tapering pinnae (*de Nevers et al. 6290*).—16. Part of rachilla, showing absence of hairs (*de Nevers 5550*). Scale bar = 250 µm.*

de Nevers & Herrera 8029 (CAS, MO); Cerro Obu, 78°48′W, 9°23′N, 25 June 1986, *de Nevers & Herrera 8055* (CAS, MO).

Prestoea semispicata is unusual in the genus by the usually spicate inflorescence, seeds with homogenous to slightly ruminate endosperm, and shape of the pinnae. In populations where individuals with branched inflorescences occur, spicate inflorescences are also found. In fact, branched and spicate inflorescences form on the same plants. *Prestoea semispicata* appears morphologically similar to that group of *Prestoea* characterized by a weakly developed stem, absence of crownshaft, markedly unequal prophyll and peduncular bract, short rachis with few rachillae, and seeds with either homogenous or ruminate endosperm (Henderson, 1986). In this group, *P. semispicata* shares with *P. cuatrecasasii* and *P. schultzeana* (Burret) H. Moore seeds with homogenous endosperm but differs in the shape of the pinnae and in having usually spicate inflorescences. Some specimens of *P. longipetiolata* from Nicaragua and *P. pubens* H. Moore from Colombia have two or three rachillae on the inflorescence, but these are densely tomentose and not glabrous as in *P. semispicata*.

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KARYOTYPE VARIATION IN *PANCRATIUM HIRTUM* A. CHEV. (AMARYLLIDACEAE)[1]

S. O. Oyewole[2]

ABSTRACT

Natural populations of Pancratium hirtum *A. Chev. from different ecological niches show definable morphological variation. Samples were grown in an experimental garden and investigated karyotypically. Five morphological variants (morphotypes) were identified and were confirmed as showing karyotype differences. Karyotype differentiation involves at least: (1) chromosomal breakages, and (2) differences in the total length of chromatin material per nucleus. The chromosome basic number of* x = *11 is confirmed for the species, while the presence of accessory chromosomes in one morphotype is reported for the first time in the genus. Population divergence is less pronounced than karyotypic divergence.*

Pancratium L. is represented in West Tropical Africa by two species, *P. hirtum* A. Chev. and *P. trianthum* Herb. Their taxonomy was well documented by Morton (1965), who reported the somatic chromosome number of $2n = 22$ for them. Morton did not include analysis of the karyotypes. *Pancratium hirtum*, with large chromosomes, is especially suitable for study of chromosome morphology.

MATERIALS AND METHODS

Pancratium hirtum grows in a variety of niches in savanna vegetation, where it exhibits minor but definable differences in leaf size, leaf color, extent of pubescence, length and form of the peduncle, and texture of the outermost tunic of the bulb (Table 1).

Five morphological groups (morphotypes, Fig. 1) were recognized during field study and samples were collected. Not fewer than 40 bulbs of each morphotype were grown separately on adjacent beds in the experimental garden. Their habitats are described in Table 2.

Each bulb in each morphotype was examined cytologically using root tip squashes as outlined in Darlington & LaCour (1969). Chromosome counts were made from several metaphase plates in each preparation. Measurement of chromosomes using calibrated micrometer eyepiece graticule was impracticable due to their unusual lengths. Photographs of metaphase plates were taken at ×7.5 ocular and ×40 objective of the Olympus (Vanox model) Research Microscope. Chromosomes were measured from the photomicrographs. The measurements were pooled from 15–20 complements for each morphotype, and average lengths were determined. Chromosome morphological determinations were according to Levan et al. (1964) as modified by Adhikary (1974). Evidence of chromosomal changes was manifested in unequalness of members of homologous chromosome pairs (such changes usually affect one arm of a member). In such instances, the unaffected arm length was employed to identify the members, and the chromosome index was based solely on the length of the longer member of the pair. Idiograms were constructed from enlarged photomicrographs.

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RESULTS

Karyotype data are summarized in Table 3. Figure 2 shows metaphase plates of the somatic complements, and Figure 3 presents the idiograms. All morphotypes have a somatic chromosome number of $2n = 22$, except E, in which the complement is $2n = 22 + 4$ B-chromosomes.

Morphotype A. The chromosomes vary in length from 5.5 μm to 19 μm, with a total length of chromatin material of 216.5 ± 6.5 μm. The complement (Figs. 4A, 5A) consists of four pairs with median to submedian centromeres (1st, 2nd, 3rd, and 11th), one telocentric pair (8th), and six pairs with terminal to subterminal centromeres (4th–7th, 9th and 10th). The longest two pairs have unequal members, one member of each having lost a portion of its long arm.

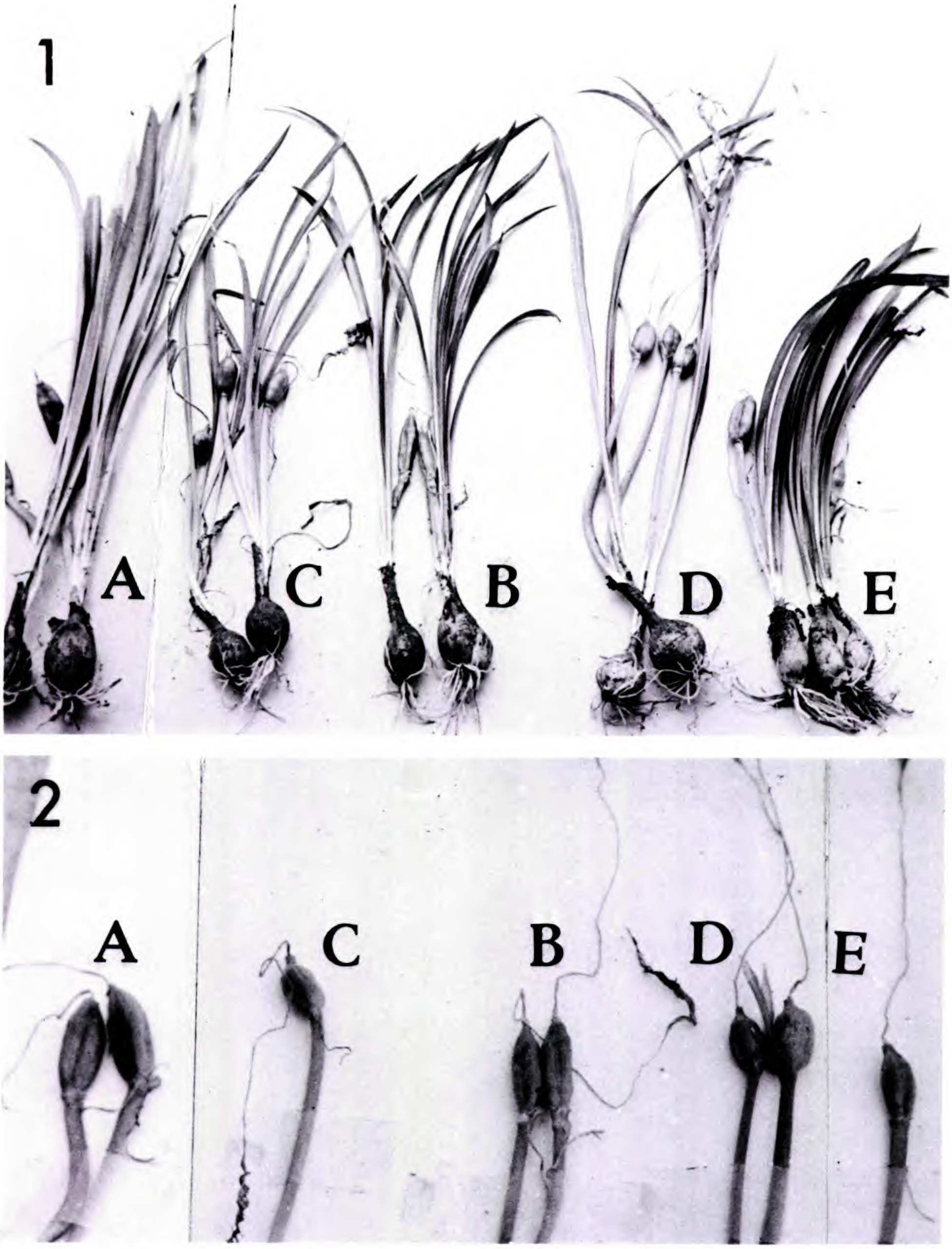
Morphotype B. Chromosomes vary in length from 11.38 μm to 41.75 μm, with an average total chromatin length of 439.5 ± 18.5 μm. The complement (Figs. 4B, 5B) consists of three pairs (1st, 2nd, and 11th) with median to submedian centromeres, and eight (3rd–10th) with terminal to subterminal centromeres. The second- and third-longest pairs have unequal members: a member of the former having lost a portion of the long arm, while one member of the latter lost a portion of its short arm.

Morphotype C. Chromosomes vary in length from 6.3 μm to 19.14 μm, and the total chromatin length averages 237.3 ± 23.3 μm. The complement (Figs. 4C, 5C) consists of three pairs (1st, 2nd, and 11th) with median to submedian centromeres and eight pairs (3rd–10th) with terminal to subterminal centromeres. The third-longest pair has unequal members—the shorter member has a shorter second arm. One member of the shortest pair also shows loss of a portion of one arm.

Morphotype D. Chromosome length varies between 8.6 μm and 27.3 μm, with an average total chromatin length of 340.4 ± 49.8 μm. The complement (Figs. 4D, 5D)

TABLE 1. *Summary of the external morphology of* Pancratium hirtum *morphotypes.*

	A	B	C	D	E
Peduncle	4–7 cm long, flattened, puberulous	2–4.5 cm long, elliptic, fluted, faintly puberulous	4–7 cm long, cylindrical, glabrous	10–13 cm long, cylindrical, glabrous	4–6 cm long, slightly flattened, shortly puberulous
Fruit	2.5–3.5 cm long, 3–3.6 cm circumference, oblong-elliptic, obtuse apex, trigonal in transverse section, green, glabrous, receptacle 1–3 mm high	2–4 cm long, 2–3.3 cm circumference, lanceolate, obtuse apex, trigonal in transverse section, green, glabrous, receptacle 1–3 mm high	1.7–2 cm long, 2–3.6 cm circumference, oblong, apex 4–5 mm high, trigonal in transverse section, green, glabrous, receptacle 1–3 mm high	1.4–2 cm long, 2.5–3.5 cm circumference, cylindrical, apex 2–4 mm high, trigonal in transverse section, green, glabrous, receptacle 1–3 mm high	2–2.5 cm long, 3–4 cm circumference, spindle shaped, apex 1–5 mm high, obtusely trigonal, green, glabrous, receptacle 1–3 mm high
Leaf	light green, 26–33 cm long, 9–15 mm wide	dark green, 21–30 cm long, 4–9 mm wide	light green, 22–31 cm long, 5–9 mm wide	light green, 24–35 cm long, 5–9 mm wide	dark green, 20–26 cm long, 7–14 mm wide
Bract	single, deciduous, about half-encircling, single lipped, yellowish green	single, deciduous, half-encircling, single lipped, green	single, deciduous, half-encircling, single lipped, light green	single, persistent until fruit ripening, fully encircling, 2-lipped, green	single, deciduous, half-encircling, single-lipped, dark green



FIGURES 1, 2.—*1.* Pancratium hirtum *morphotypes with mature fruits, ×0.2.—2. Mature fruits, with peduncles, of* Pancratium hirtum *morphotypes, ×0.4.*

consists of five pairs (1st–3rd, 10th, and 11th) with median to submedian centromeres and six pairs (4th–9th) with terminal centromeres. Five of the eleven pairs (1st, 2nd, 3rd, 8th, and 10th) show evidence of loss of portions from one member of each pair. First and 10th pairs show loss in the long arm; the second and third pairs show loss in the short arm, and the eighth shows loss in one of the two equal arms.

Morphotype E. The autosomes vary in length from 5.6 μm to 17.9 μm, and the B-chromosomes vary between 1 μm and 1.5 μm. The average total chromatin length is 219.14 ± 2.5 μm. The complement (Figs

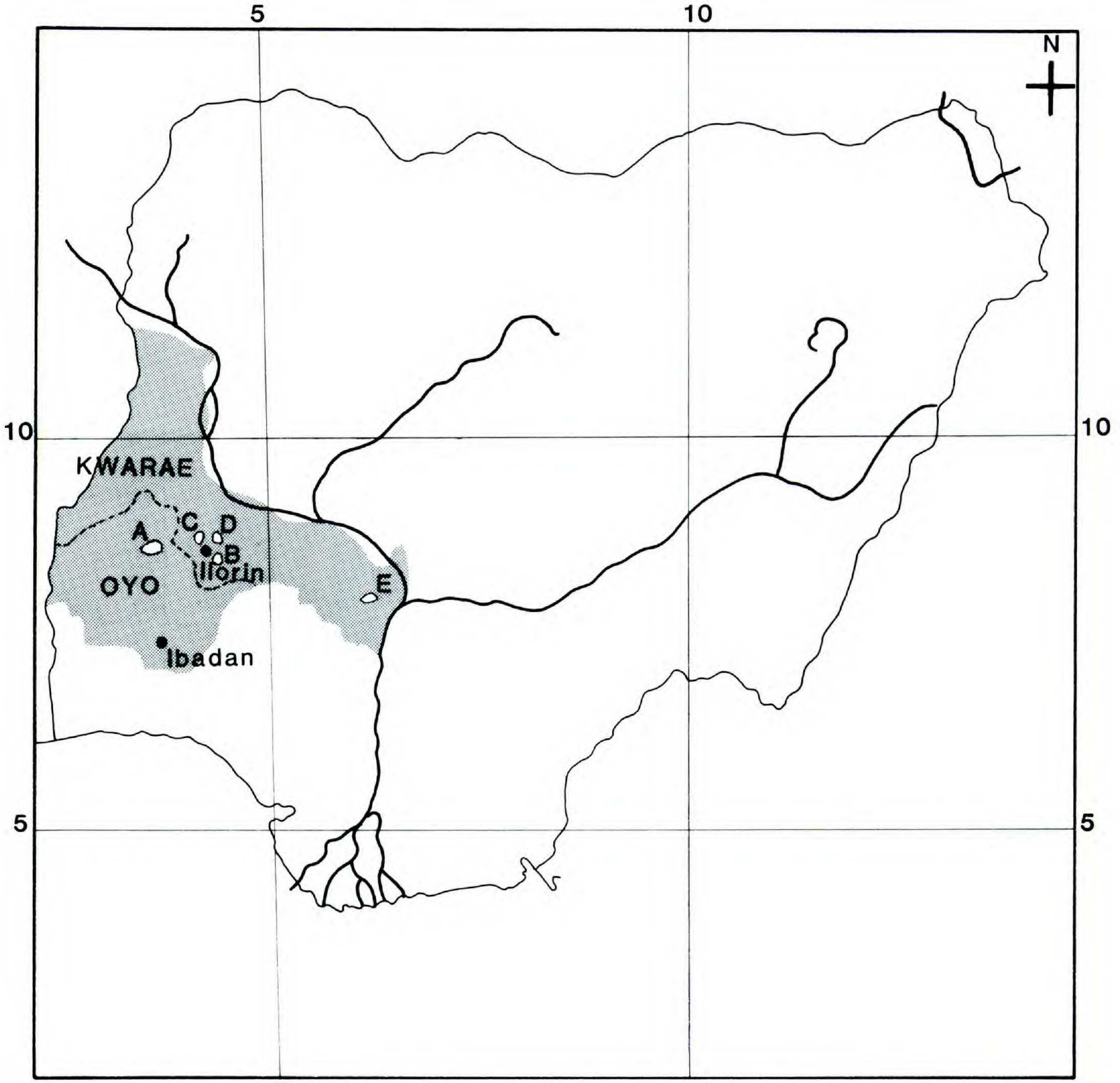


FIGURE 3. *Map of Nigeria showing locations where* Pancratium hirtum *populations were sampled in Oyo and Kwara States. Broken line = state boundary; circles = state capital city; solid lines = rivers.*

4E, 5E) consists of five pairs (1st, 2nd, 4th, 8th, and 11th) with median to submedian centromeres, and six pairs (3rd, 5th, 6th, 7th, 9th, and 10th) with terminal to subterminal centromeres. All the B-chromosomes are telocentric. One member of the second-longest autosomal pair has chromosome loss in the long arm, while one member of each of the eighth and ninth pairs shows loss in the short arm.

DISCUSSION

Previous chromosome counts in *Pancratium* show a chromosome number of $2n = 22$ (Ponnamma, 1978; Lakshmi, 1980). This number is confirmed here except that the presence of accessory chromosomes had not been reported previously in the genus.

The five karyotypes share a basic plan: the largest two and the smallest pairs of chromosomes are metacentric while all the others are acrocentric. Deviations from this plan consist of increase in the number of metacentrics (A, D, and E with an increase of one, two, and two pairs, respectively). Apart from these, there is evidence of structural changes in the chromosomes as a result of loss or gain of segments. This is common to all the karyo-

TABLE 2. *Sources of material of* Pancratium hirtum.

Morphotypes	Collection Site	Herbarium Voucher	Habitat
A	Iseyin–Igbetti about 150 km northwest of Ibadan	S00/2106 in University of Ilorin Herbarium (IUH)	deciduous woodland, in dark humus, under the shade of trees such as *Butyrospermum paradoxum*, *Lophira lanceolata*, etc.
B	Affon, 25 km southeast of Ilorin	S00/2199 in IUH	disturbed woodland, in dark humus soil on shallow inselbergs and foot of rocky hill under the shade of *Parkia biglobosa*
C	Shao, 22 km northwest of Ilorin	S00/2200 in IUH	open and exposed brown soil of old mats of *Afrotrilepis pilosa* on rock outcrops in savanna grassland
D	Oke-Oyi, about 20 km north of Ilorin	S00/2201 in IUH	open brown humus soil among rock boulders in savanna grassland
E	Okene–Lokoja Road, about 50 km from Okene	S00/2202 in IUH	dark brown gravelly clay–loam in floodplains in savanna woodland under stands of *Khaya senegalensis*

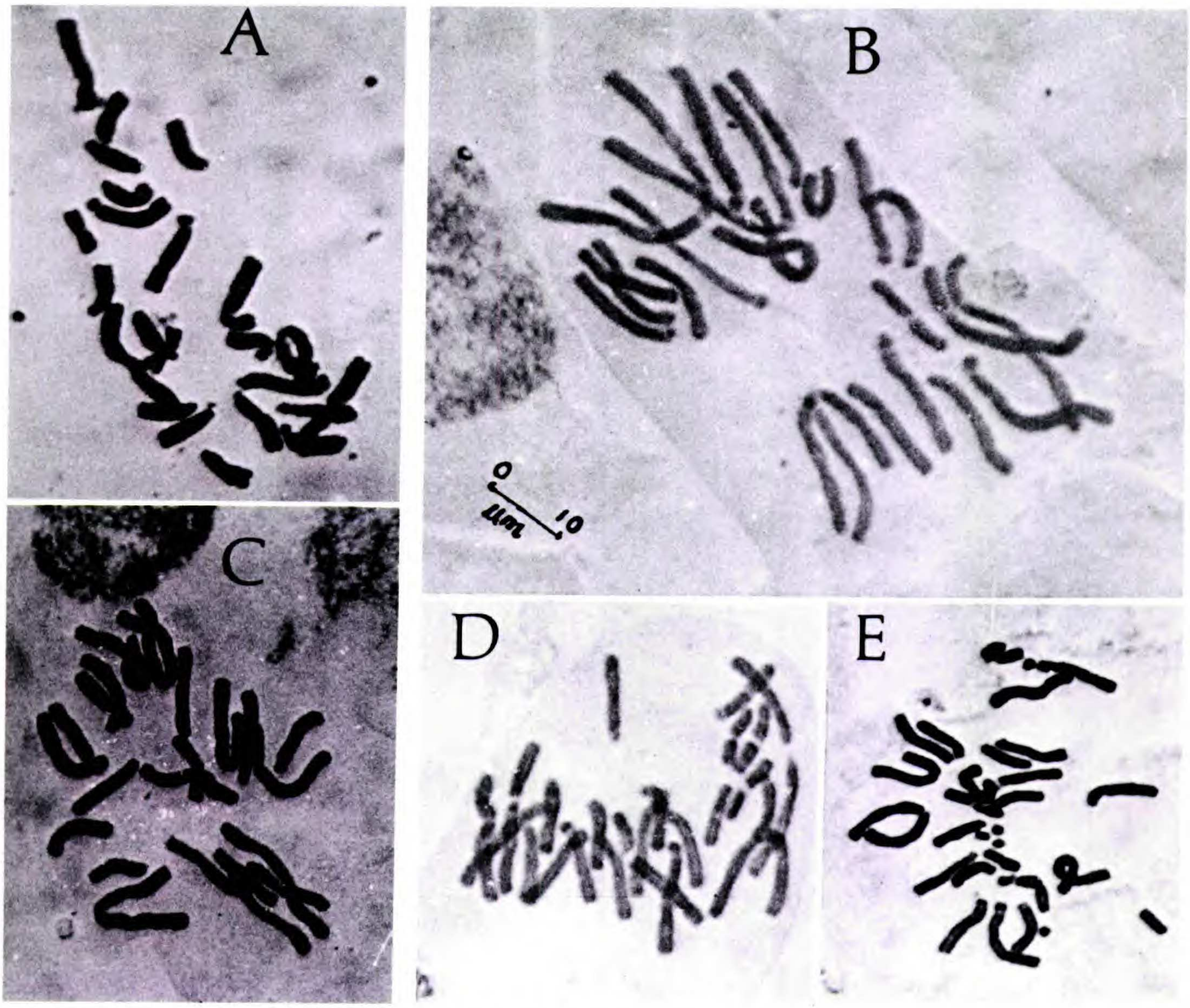


FIGURE 4. *Somatic metaphase complements of* Pancratium hirtum *morphotypes.*

TABLE 3. *Karyotype data for* Pancratium hirtum *(chromosome length in μm).*

Homologues		A	B	C	D	E
1	chromosome length	19.0	41.75	19.14	27.25	17.88
	r-value	1.1	1.2	1.0	1.17	1.37
	centromere location	median	median	median	median	median
2	chromosome length	16.0	27.25	15.42	25.80	14.5
	r-value	1.0	1.37	1.76	1.48	1.7
	centromere location	median	median	median	median	median
3	chromosome length	12.25	25.75	13.92	21.06	12.63
	r-value	2.3	3.29	3.64	2.56	11.25
	centromere location	submedian	subterminal	subterminal	submedian	terminal
4	chromosome length	10.75	21.25	11.92	17.75	11.88
	r-value	9.75	13.17	10.92	10.83	1.97
	centromere location	terminal	terminal	terminal	terminal	submedian
5	chromosome length	9.0	18.75	9.75	15.0	9.0
	r-value	8.0	14.0	13.63	10.25	35.0
	centromere location	terminal	terminal	terminal	terminal	terminal
6	chromosome length	7.5	16.0	9.25	13.0	8.25
	r-value	14.0	15.0	21.2	11.0	15.5
	centromere location	terminal	terminal	terminal	terminal	terminal
7	chromosome length	7.5	15.5	9.0	12.0	8.25
	r-value	14.0	14.5	8.0	13.4	7.25
	centromere location	terminal	terminal	terminal	terminal	terminal
8	chromosome length	7.0	15.0	8.58	10.92	7.38
	r-value	0	9.0	7.58	17.71	2.04
	centromere location	terminal	terminal	terminal	terminal	submedian
9	chromosome length	7.0	14.0	8.0	10.75	6.63
	r-value	6.0	13.0	11.0	13.33	3.0
	centromere location	subterminal	terminal	terminal	terminal	subterminal
10	chromosome length	6.75	13.13	7.33	10.0	6.25
	r-value	26.0	16.5	21.0	1.07	4.0
	centromere location	terminal	terminal	terminal	median	subterminal
11	chromosome length	5.5	11.38	6.33	8.67	5.67
	r-value	1.2	1.12	1.0	1.0	1.2
	centromere location	median	median	median	median	median
Accessory chromosomes		—	—	—	—	1.5, 1.0
		—	—	—	—	1.0, 1.0
	total chromatin length	216.5 ± 6.5	439.5 ± 18.5	237.3 ± 23.3	340.4 ± 49.8	219.14 ± 2.5

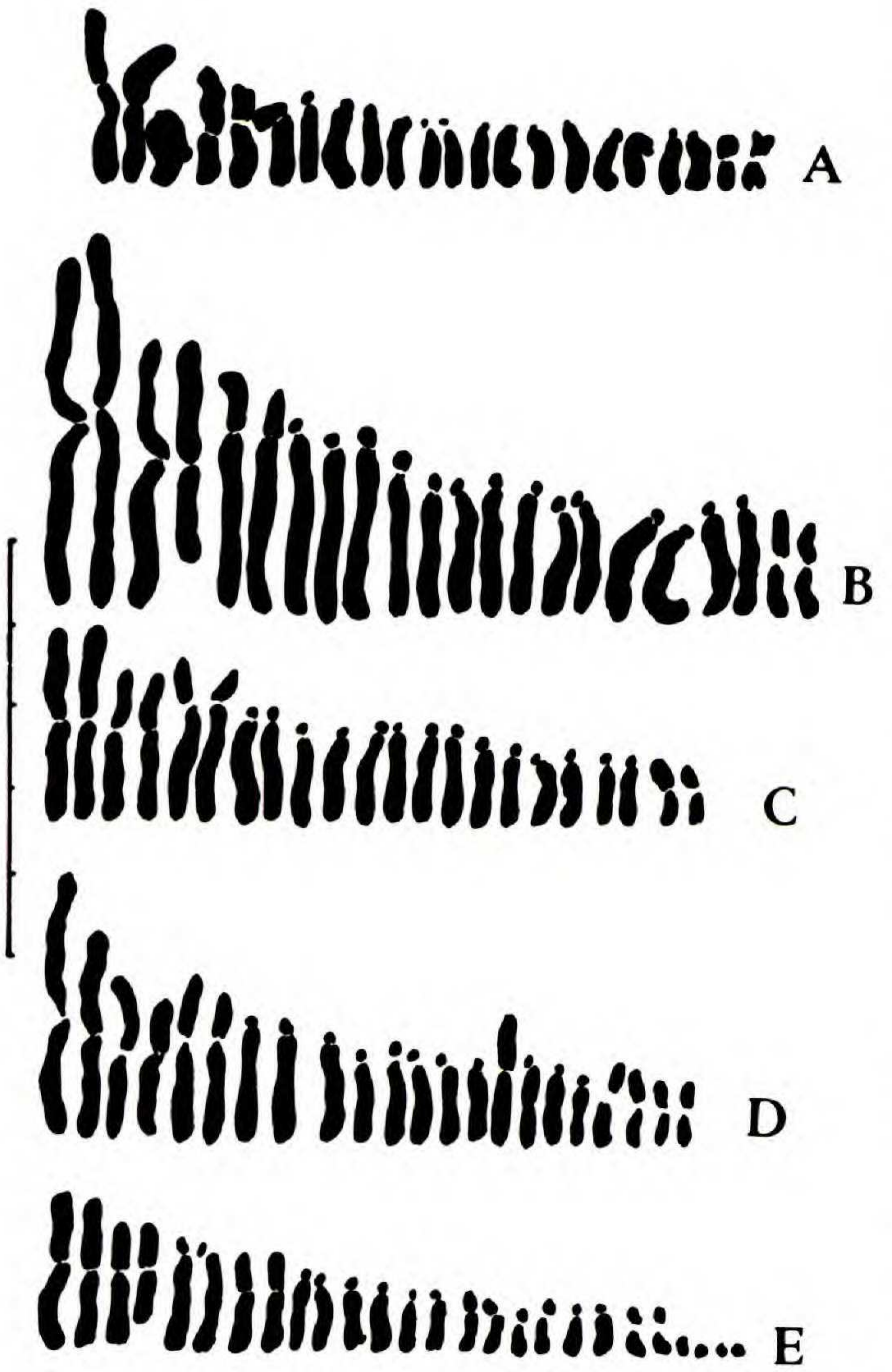


FIGURE 5. *Idiograms of the somatic chromosome complements of* Pancratium hirtum *morphotypes.*

types. Further deviation is the presence of B-chromosomes in E.

One way of generating genetic variation is by changes in chromosomal morphology, which are reflected in the karyomorphology of the population or the species (Coates, 1979; Coates & James, 1979). Another way is by genic changes that may not be immediately detectable (see Linhart et al., 1981). Thus, while genic changes may not be as immediately detectable as changes in the karyotype, karyotype variation may not be immediately accompanied by morphological divergence.

Karyotype variation in *P. hirtum* is associated with population differentiation and ecological preference. Dickinson & Antonovics (1973) maintained that karyotypic differentiation is a direct response of various biotypes to differing habitat pressures. White (1973) opined that chromosome rearrangements underlie reproductive isolation and, hence, speciation. It is probable that the ancestral population of *P. hirtum* in West Africa was at some time afflicted by some drastic environmental events that left survivors whose genetic systems suffered some changes. Such survivors occupied different ecological niches to which each had adapted for continued survival. Each has thus become ecologically isolated. Such a situation would be reinforced further by environmental barriers to long-distance pollen dispersal. The smallness of the population that would initially inhabit each ecological niche would enhance both chromosomal evolution and speciation, as asserted by Wright (1940), Bush et al. (1977), and Bengtsson (1980). These events would lead to reproductive isolation and thereby lay the foundation for further divergence of the population, culminating, in time, in the formation of several species. Again, the effects of the environment, especially edaphic factors, may be the major driving force in the karyotypic differentiation in this species. For instance, Morton's (1965) pl. 14, fig. 1 is similar to the karyotypes reported here, but it is not identical with any of them. All of Morton's materials were collected from Ghana. It is therefore possible that other karyotypes may still be encountered within the tropical West African region.

In conclusion, karyotype differentiation in *P. hirtum* has involved: (i) changes in chromosomal morphology resulting from loss or gain of chromosomal segments, which might have been accompanied by changes involving rearrangements of genes and/or gene blocks in inversions and translocations; and (ii) variations in the length of total chromatin material per somatic nucleus. Therefore, it seems likely that ecotype differentiation at the morphological level appears genetically fixed, and this is accompanied by varying degrees of karyotypic change, which presumably originated once the ecotypes had become established.

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THE ARCHITECTURE OF INFLORESCENCES IN THE MYRTALES[1]

Focko Weberling[2]

In Memory of Dorothea Weberling,
April 25, 1928–February 2, 1988.

ABSTRACT

In the Myrtales a great variety of inflorescences are found. In some families such as Oliniaceae or Alzateaceae (formerly included into Lythraceae) the inflorescences are exclusively of the more primitive monotelic type. In others gradual transitions from the monotelic to the polytelic type can be observed. Within the Lythraceae the genera Lawsonia, Lagerstroemia, *and* Galpinia *and—if included as subfamilies—the Punicoideae and Sonneratioideae still represent the monotelic type, whereas in the majority of the genera polytelic inflorescences are found. These often show a botrytic ramification, although the basic type of ramification is a thyrse. Among the great diversity of forms the gradual specialization of a short shoot–long shoot system can be observed, especially in the genus* Ginorea. *The same can be seen within the Combretaceae, which are polytelic throughout. As in most Myrtales families, phylloscopic accessory buds or branches are frequently occurring and sometimes form a determinating factor for the shape of a flowering plant. In Onagraceae polytelic structure of inflorescences is also manifested throughout the family and florescences as botrya or spikes are known. On this basis an impressive diversity exists, especially in the variations of the proportions between the terminal main florescence and the extension of the enrichment zone, the number and size of paracladia, the length of the internodes, and the possibility of a reversion of the inflorescence apex to vegetative growth, commonly called proliferation. The latter often occurs in the inflorescences of Myrtaceae in which the "central type" and perhaps the phylogenetically primitive form is a monotelic thyrsoid or a panicle. Even in proliferating or in truncate synflorescences the monotelic character is evident by the fact that all paracladia, including those with more than one pair of flower-bearing branches, are provided with a terminal flower. The effloration of the proliferating inflorescence can be delayed for such a long time that the proliferating shoot may even form branches above the flower-bearing zone. Thus inflorescences of this shape sometimes were regarded as "intercalary inflorescences." In some cases (some species of* Eugenia*) the transition to the polytelic type seems to be complete. In the majority of the Penaeaceae the inflorescences forming thyrsoids or stachyoids follow the monotelic type. Some facultatively or constantly truncate synflorescences form a transition to taxa with polytelic synflorescences. In Psiloxylaceae the flower-bearing systems are brachyblasts reduced to their botrytic florescence and inserted on older axes. Variety of inflorescences in Melastomataceae corresponds to the size of the family but shows less diversity than Myrtaceae. The inflorescences are monotelic. Cases of complete transitions to polytelic structures were not found. Even truncation seems to be rare and only a single case is reported for* Medinilla magnifica. *On the other hand, proliferation is not rare.*

FUNDAMENTAL FEATURES OF INFLORESCENCE MORPHOLOGY

Since differences and conformities in the arrangement of flowers are characteristic for smaller or larger taxonomic groups, these criteria have been used in many ways since the very beginning of systematic botany. For this purpose an elaborate descriptive terminology is in use designating the different modes of foliation and especially of ramification by well-known terms such as raceme, spike, umbel, panicula, etc. Many efforts have been made to establish a natural system for the immense diversity of inflorescences. The results, however, remained insufficient, primarily because the empirical basis was too small. Above all, it does not follow that the flower-bearing parts

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to which a term such as "spike," "umbel," or "dichasium" is applied are necessarily homologous. For that reason, one cannot achieve correct interpretation of the morphology of inflorescences by focusing exclusively on those flower-bearing ramification systems that by some conspicuous quality appear to be "units." One must also consider the position of these entities within the structural plan of the whole plant. Only in this way it is possible to ascertain which flower-bearing elements may legitimately be compared as identical structures. This, however, is connected with the elucidation of the structural plans of flowering plants and therefore needs a broad empirical basis. According to Troll (in Troll & Weber, 1955; Troll, 1964, 1969), the great diversity of inflorescences is due to the variation of two types only: the polytelic and the monotelic types.

In the *monotelic* inflorescence (Fig. 1 I), the apex of the inflorescence axis commonly ends with a *terminal flower*. This also applies to all the floral branches below the terminal flower. All of these branches, whether branched or not, are homologous elements, and they are all referred to by the term *paracladia* (pc; singular: paracladium), because these branches repeat the structure of the main axis of the flowering system. Accordingly, their ramifications are called paracladia of the second to n^{th} order. The whole area that produces flowering paracladia (Bereicherungstriebe, "enriching branches") may be designated as the *enrichment zone* (Bereicherungszone, "paracladial zone"). In the lower part of the flowering shoot this zone is commonly preceded by an *inhibition zone*, within which the development of paracladia is inhibited more or less abruptly (Figs. 1, 3 I). The same zonation can be recognized in the individual paracladia if these are not reduced in any way. In perennials the axillary buds at the base of the whole stem do not develop within the same season but will give rise to innovation shoots at the beginning of the following season. Therefore, this area has to be distinguished as an *innovation zone*.

In the *polytelic* type of inflorescence (Fig. 1 II), which is no less frequent in angiosperms, there is no terminal flower at the summit of the primary axis. The shoot apex remains *indefinite* after developing a smaller or greater number of lateral flowers, the last of which often do not complete their development but atrophy in the same way as the end of the axis. This apical flowering system, which is composed of lateral flowers only (or cymes, see below), is a characteristic feature of this type of inflorescence and is now referred to by the special term *florescence*. The term "florescence" should not be confused with the term "*in*florescence," which has no specified morphological signification and may be used to designate any flower-bearing ramification system. (The same applies to the term "partial *in*florescence," which can designate without any morphological relevance any part of a flowering system, while the term "partial florescence" means a distinct part of a florescence, namely a cymose branch.) Instead of ending in a single flower, as in the monotelic inflorescence, the floral axis here terminates in a multiflowered so-called polytelic florescence.

If the lateral flowers composing the florescences are provided with prophylls (Fig. 2 I), these may produce secondary flowers or dichasial or monochasial flowering systems from their axils (Fig. 2 II). This mode of ramification, in which the production of branches is restricted to the axils of prophylls of consecutive order, is called cymose (see Schimper, 1835; Wydler, 1851a: 305 ff.; Eichler, 1875: 34 ff., but not in the strict sense; Troll, 1957: 234 ff.; 1964: 63). The diverse sympodial ramification systems resulting from this mode of branching (Fig. 2 III–VI) are often briefly called cymes (cymae, see p. 231). In such cases the florescence consists of cymose *partial florescences* (pf) as, for example, in the inflorescences of most Scrophulariaceae and Labiatae (Fig. 3 III). Within both families, the derivation given here is verified by many transitional forms.

Below the florescence terminating the main axis there may be some branches that repeat the structure of the main stem by producing

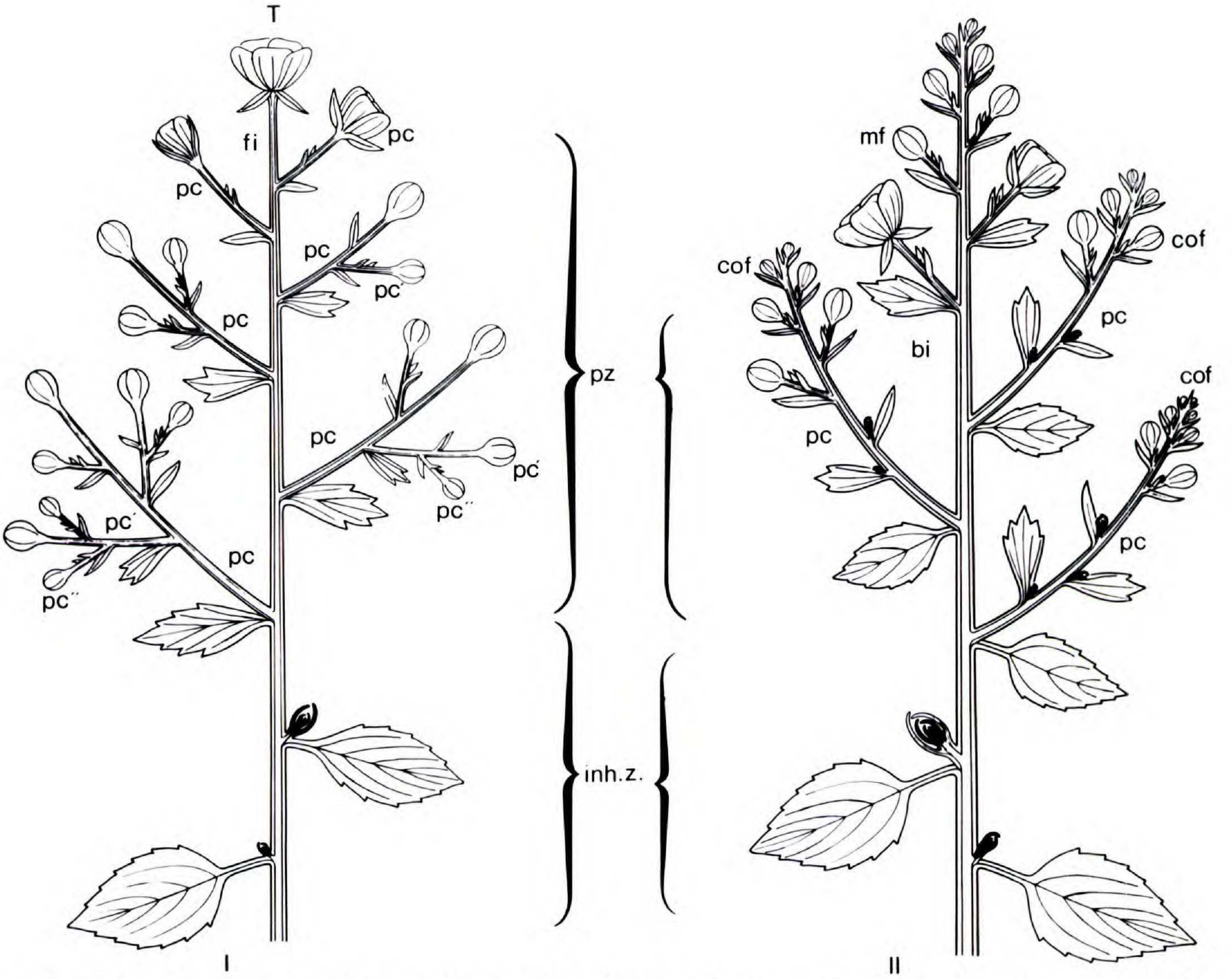

FIGURE 1. *Diagrams of a (I) monotelic and (II) polytelic inflorescence. T, terminal flower; pc, paracladium; pc', pc", paracladia of second and third order; mf, main florescence ("Hauptfloreszenz"); cof, co-florescence; bi, basal internode ("Grundinternodium"); fi, final internode ("Endinternodium"); pz, paracladial zone ("Bereicherungszone"); inh.z. inhibition zone ("Hemmungszone"). From Troll (in Troll & Weber, 1955), slightly modified.*

florescences themselves and that therefore are also called *paracladia.* Their florescences are termed *co-florescences* in order to distinguish them from the main florescence of the main axis. The apices of the co-florescences remain *indefinite* like those of the main florescence. Thus the whole flower-bearing ramification system appears as a system of florescences: a (polytelic) *synflorescence.* In the case of a monotelic inflorescence, the synflorescence consists of a terminal flower and (monotelic) paracladia.

Within the polytelic synflorescences, the same zonation can be observed as in monotelic flowering systems (Fig. 3 II, III): an *enrichment zone* (Bereicherungszone: Troll), which precedes the main florescence, an *inhibition zone* (Hemmungszone: Troll), and in perennials, an *innovation zone.* The three zones together form the so-called *hypotagma.* The florescence is separated from the paracladial zone by a *basal internode* (Grundinternodium: Troll), which may be of remarkable length.

It also proved to be useful to designate the ultimate internode preceding the terminal flower of a monotelic system by a special term: *final internode* (Grundinternodium, Fig. 1 I).

The polytelic type probably has been derived repeatedly from the monotelic during the evolution of angiosperms *by reduction of the terminal flower* and *specialization of the paracladia* of the monotelic system into either single lateral flowers or lateral cymes, which then constitute elements of the florescences, whereas the others are differentiated as par-

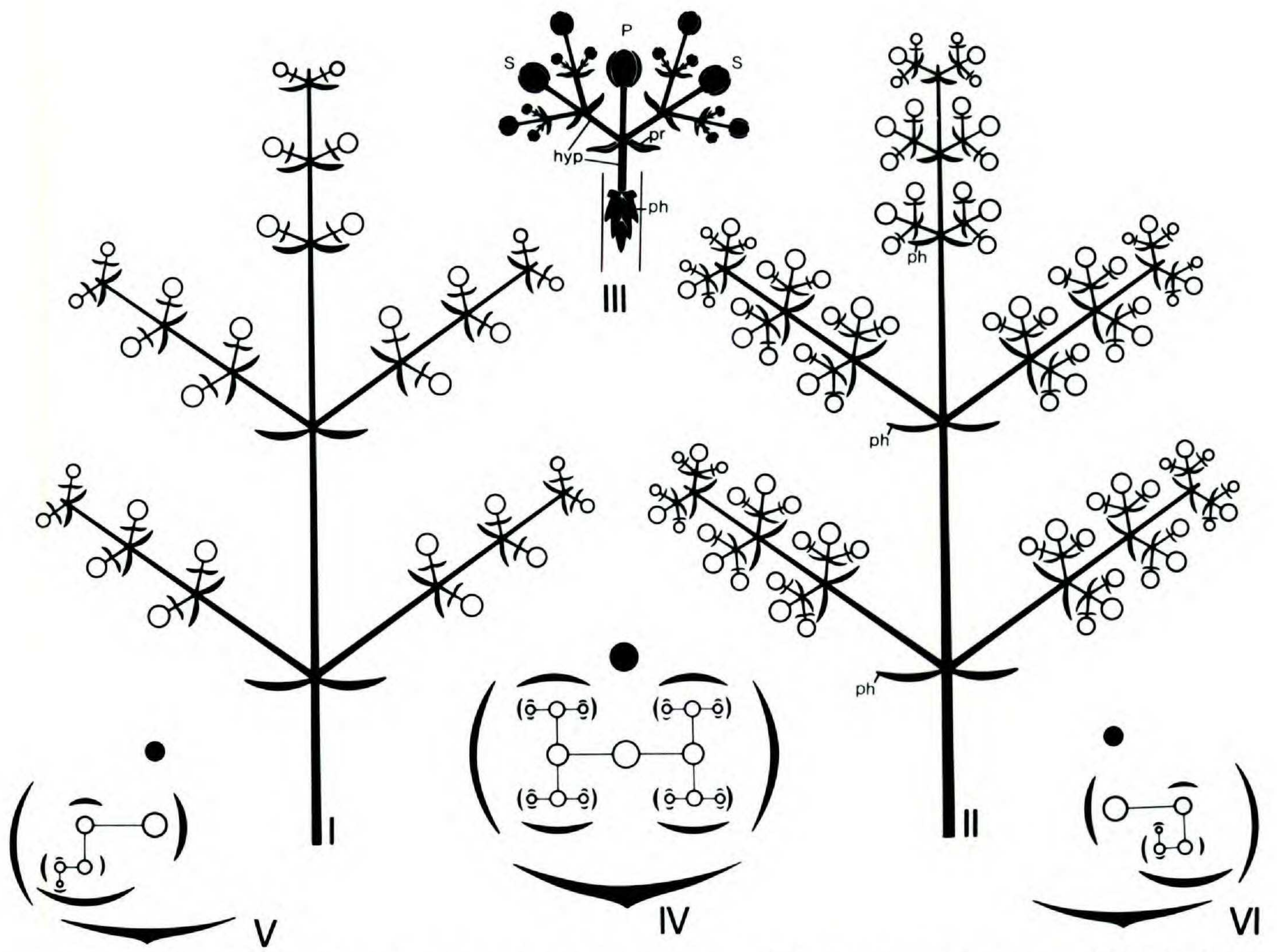

FIGURE 2. *I, II. Vertical diagrams of polytelic inflorescences.—I. Heterothetic diplobotrys.—II. Diplo-thyrse; this inflorescence can be deduced from the diplobotrys in I by the assumption that the prophylls of second order are fertile. III–VI. Vertical (III) and transverse (IV) diagrams illustrating diverse forms of cymose ramification.—III, IV. Dichasium.—V, VI. Monochasia.—V. Scorpioid cyme (cincinnus).—VI. Helicoid cyme (bostryx). P, primary flower; S, secondary flower; ph, pherophyll ("Tragblatt," "Deckblatt"); pr, prophyll; hyp, hypopodium. III–VI from Troll (1959b), modified.*

acladia (of the polytelic type), which themselves form florescences (Weberling, 1961, 1965, 1983a, b; Troll & Weberling, 1966).

In both monotelic and polytelic types, the different elements may vary in many different quantitative respects according to the principle of variable proportions: in polytelic synflorescences, the main florescence may be extended and the number of its flowers may be increased in many ways, or it may be reduced or even be missing altogether (truncate polytelic synflorescences). In both cases the paracladia may be well developed or reduced, their number may be increased, or they may be missing or modified in different ways. The development of paracladia may be basitonic or acrotonic (see below). Variation also exists in the diversity of phyllotaxis and foliation, shortening or lengthening of the internodes in different parts of the plant, different intensity and different modes of ramification, and so on. Especially in woody plants the zonation of flowering systems can be altered extremely by, for example, the complete reduction of the inhibition zone.

An essential difference between the types seems to be that in inflorescences of the polytelic type the shoot apex of the inflorescence axis remains indeterminate. This also occurs, however, in some monotelic inflorescences in which the terminal flower aborts. In such *truncate monotelic synflorescences*, however, the paracladia usually end in terminal flowers, thus demonstrating the monotelic character of the whole system.

In many lianas, the growth of the main

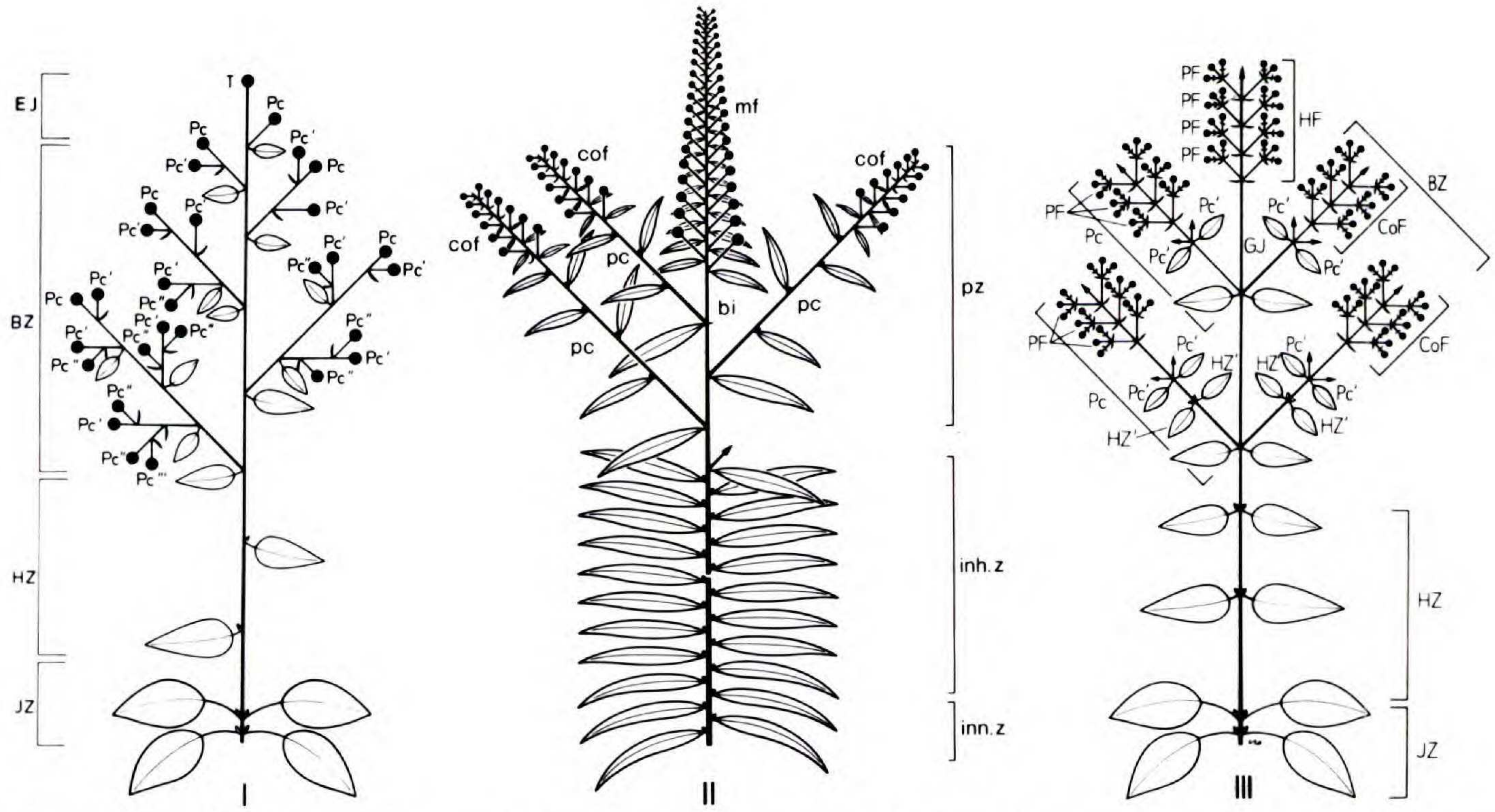

FIGURE 3. *I. Diagram of a monotelic inflorescence in form of a panicle. T, terminal flower; Pc, Pc', Pc'', Pc''', paracladia of first to fourth order; EJ, final internode ("Endinternodium"); BZ, pz, paracladial zone (enrichment zone); HZ, inh.z., inhibition zone; JZ, inn.z., innovation zone.—II, III. Diagrams of polytelic inflorescences with the main florescence (HF, mf) and the co-florescences (cof) in form of botrya (II) or of thyrses (III). GJ, bi, basal internode; pc, pc', paracladium of first and second order; HZ', inhibition zone of pc; PF, partial florescence; the rest as in I.*

axis is indefinite. Therefore the main axis, though it may produce lateral flower-bearing branches, never ends in a terminal flower. The sample applies to rosette geophytes with indefinite main axes, as in *Plantago* or *Phyllactis* (Valerianaceae). In the latter, the apex of the rosette changes periodically from the formation of absolutely sterile zones to the formation of fertile regions, in which thyrsoid "partial inflorescences" originate from the axils of the rosette leaves. (The same applies to the so-called *proliferating inflorescences* of many Myrtaceae.) In cases like these, the monotelic or polytelic character of the inflorescence is revealed by the monotelic or polytelic character of the paracladia.

Thus the question of whether the terms monotelic and polytelic correspond to the old classification of inflorescences into two groups called "indeterminate" (indefinite, racemose) and "determinate" (definite, cymose) must be answered in the negative. Apart from this answer, the statement given by Rickett (1955: 419), that "current usage" of this classification, "at least in English, is both confused and inaccurate," still refers to this classification in general. To a great extent this is due to the fact that the "cymose type" is often equated with an "overtopping" of the (somewhat sympodial) branching system (Rickett, 1955: 426; Goebel, 1931: 81 ff.).

However, it is neither necessary nor possible to renounce all the classical descriptive terms used for the description and distinction of flower-bearing ramification systems. Many of these terms can be used without any change, and some need to be clarified and specified in their application. This also has been done by Troll (1964: 33 f.), who partly referred to Eichler (1875: 34 f.) in his classification of descriptive terms, which may be repeated here:

I. *Simple inflorescences:* botrys (raceme), spike (stachys), spadix, umbella, capitulum.
II. *Complex (compound) inflorescences*
    a. with racemose partial inflorescences: diplobotrys (and related forms: bispica, bi-umbella, etc.), panicula.

b. with cymose partial inflorescences: thyrse (including thyrsoid), cymoid.

Among the compound inflorescences the panicle is distinguished by the main axis ending in a terminal flower (as do all of the branches). Thus the panicle is a determinate inflorescence, and this term never refers to any indeterminate inflorescence, as it often is used by English language authors.

If all branches of the panicle are reduced to single flowers (uniflorous paracladia), a botryslike system results that, however, still ends in a terminal flower and therefore is termed a "botryoid"; if the flowers are sessile, a spicoid. Complete reduction of all lateral flowers (all paracladia) leads to a uniflorous system (single terminal flower).

The term thyrse, which was often confused with the term panicle (Čelakovský, 1893: 45), needs some further comments too. (There is, of course, some connection between panicles and thyrsoids, as seen, e.g., in the so-called thyrso-paniculate systems of *Sambucus* and *Viburnum*: Troll & Weberling, 1966.) The term, used by Linnaeus for a "coarctate panicle of ovate form" (Rickett, 1955: 443), was specified by De Candolle (1827: 417) as "compound of small cymes along an axis of indefinite growth" (Rickett, 1955: 443; Bravais & Bravais, 1837: 197: "groupe de cimes disposées d'après l'évolution centripète comme les fleurs le sont dans l'épi"). It was applied, however, to determinate thyrsic branching systems as well (see Troll, 1964: 63 f.).

Briggs & Johnson (1979: 177, 247) restricted the term thyrse to a "blastotelic inflorescence with a multinodate main axis that bears lateral cymes"; thus a determinate thyrselike ramification system should be termed a thyrsoid (which appears consequent, as this term is comparable with terms such as botryoid, spicoid, cymoid in the terminology of Troll). Although we fear that a change of terminology used hitherto in so many publications might cause new confusion, we hesitantly follow this suggestion of Briggs & Johnson. Consequently, and in accordance with these authors, the adjective "thyrsoid" must be replaced by "thyrsoidal" (thyrsusartig), while the adjective thyrsic (thyrsisch) should be used now for a thyrse in the restricted sense.

The terms used here are illustrated by Figure 2 II–VI. The vertical diagram in Figure 2 II shows a diplo-thyrsic inflorescence. The distal part of it, comprising three pairs of lateral cymes, forms a simple thyrse (monothyrsus, haplothyrsus), whereas the branches originating from the two proximal nodes are thyrses themselves (named "Spezialthyrsen" by Troll, "special thyrses," infrathyrse). In this diagram, the lateral cymes are triadic, i.e., comprising three flowers only. They may, however, produce more flowers by continuous branching from the consecutive axes (Fig. 2 III). The characteristic trait of this mode of ramification is that each axis before ending in a terminal flower produces two and only two leaves: the *prophylls*, which are mostly transversal-opposite and identical with the prophylls (the first two leaves) of other branches. In monocotyledons there is frequently only one prophyll, often in adaxial position. The internode preceding the prophyllar node is the *hypopodium*, the internode following the prophyllar node and terminating in the flower is the *epipodium*. If the two prophylls are separated by another internode, this is called the *mesopodium*. From the axils of the prophylls of the primary flower arise branches that end in the secondary flowers and bear two prophylls of second order. From the axils of the prophylls of second order the ramification can continue in the same way. This mode of cymose ramification can result in a complete symmetrical dichasium as shown in Figure 2 IV. In many cases, however, the continuation of the ramification is limited at a certain stage to one of the two prophyllar axils, thus resulting in the formation of a monochasium, either a scorpioid cyme (cincinnus, Fig. 2 V) or a helicoid cyme (bostryx, Fig. 2 VI). In the monocotyledons a rhipidium or a drepanium can be formed.

In thyrsoidal inflorescences, as displayed in a great variety of forms within the Caryophyllaceae for example, a high degree of diversity can result from differences between paracladia in vigor of development. In many cases the paracladia are more extensively developed toward the base of the plant (*basitonic* ramification) or, if the paracladial zone is preceded by an inhibition zone, toward the middle of the plant (*basi-mesotonic*; in *mesotonic* ramification, vigor of the paracladia increases from both ends to the middle part of the flowering system), whereas in others the distal paracladia are the most vigorous (*acrotonic* ramification). Examples for these models can be found within the genus *Silene*.

In thyrsoids with decussate foliation and ramification (as in *Silene*), extreme acrotonic branching results in the exclusive development of the uppermost pair of cymose paracladia, which far overtop the main axis by vigorous development and copious branching. Such dichasia as represented, e.g., by *Silene vulgaris* (Moench) Garcke often have been regarded as ideal "cymose inflorescences." They are, however, connected by many transitional forms with basi-mesotonic thyrsoids as represented, e.g., by *Silene nutans* L. In other plants transitions can even appear in the same individual, if the subdistal pair of paracladia develops at a later stage. Thus these "dichasial" inflorescences do not represent an inflorescence type of their own but must be regarded as thyrsoids with acrotonic ramification. The complete inflorescence only simulates a cymose ramification, which actually takes place in the cymose paracladia. This induced Troll (1959a: 115; 1964: 102) to name this extreme form of an acrotonic thyrsoid a cymoid. In similar fashion, monochasial or pleiochasial overtopping of the main axis can be included in this term.

As is well known, foliation and phyllotaxis often change in the transition from the vegetative to the flower-bearing parts of a plant. The foliage leaves may be diminished from leaflike *frondose* to smaller *frondulose* organs or even convert by change of diverse proportions into *bracteose* organs (*bracts*), which are often more or less scalelike. The subtending leaves of the flower-bearing branches, the *pherophylls* (Briggs & Johnson, 1979: 179, 246; "Tragblatt," "Deckblatt"), may thus be frondose, frondulose, or bracteose.

The *mode of efflorescence* can, but need not be characteristic for the diverse forms of inflorescences. One should expect that anthesis of flowers follows the way of their initiation, advancing from, for example, the oldest flowers at the base of a botryoid to the top of this flowering system. In monotelic synflorescences, however, the terminal flower usually blooms before the neighboring laterals. To some extent this dominant position results from the fact that the organs of the terminal flower arise from the inflorescence apex immediately, whereas the lateral flowers are formed by lateral apices. Thus the terminal flower is somewhat in advance in relation to the ultimate lateral flowers. It is not rare for the flowers or partial inflorescences in the axils of the ultimate leaves preceding the terminal flower to be retarded or even to abort. Thus the terminal flower can be preceded by sterile leaves that are called "Zwischenblätter" (Nordhagen, 1937: 12; Troll, 1964: 15) or *metaxyphylls* (Briggs & Johnson, 1979: 179, 244). Beyond that, cases of a complete basipetal efflorescence—advancing from the top to the base of a flowering system—are not rare (*Meconopsis*). In the florescences of polytelic inflorescences, the efflorescence usually advances from base to apex (acropetal). For thyrses this means, of course, that an acropetal sequence of primary flowers that open first is followed and overlapped by a secondary sequence of the secondary flowers of the cymose partial florescences (Troll, 1957: 380 f.). There are also florescences with divergent effloration, the best known example may be *Dipsacus*. However, the sequence of paracladia in polytelic systems mostly unfolds in a basipetal order. Starting with the paracladia immediately below the main florescence, the progression of unfolding usually depends on the vigor of the individual and the length of the flowering period, thus determining the extension of the paracladial zone and the inhibition zone (Troll, 1950). Nevertheless, in annual or hapaxanthic plants this progression can reach the base of the plant, and the most basal paracladia can, if they are fully developed, be the most vigorous.

ONAGRACEAE

Polytelic structure of inflorescences is manifested throughout the Onagraceae. The florescences are botrya or spikes. Even when the pedicels remain undeveloped, the inflorescences frequently (e.g., *Oenothera biennis* L., Fig. 4) look like botrya, because pedicels are simulated by the long gynoecium of the epigynous flowers. In some taxa, e.g., *Epilobium alsinoides* Cunn. subsp. *tenuipes* (Hook. f.) Raven & Engelhorn, the pedicels lengthen after anthesis. Plants in the flowering state, as shown for the case of *Epilobium angustifolium* (Fig. 3 II), usually show a clear zonation: below the main florescences there is a more or less extended enrichment zone (paracladial zone, pz) which stretches down the primary axis until the development of paracladia is inhibited. Transition between this "inhibition zone" (inh.z., Hemmungszone) and the paracladial zone may be more or less abrupt. In perennials the axillary buds at the base of the whole stem do not develop within the same season but will give rise to innovation shoots at the beginning of the following season ("innovation zone," inn.z., Innovationszone).

Diversity in appearance of the different genera and species depends highly on quantitative variations of these zones, different lengths of the internodia, and different foliation of the florescences.

The phyllotaxis can be alternate or decussate, sometimes even verticillate mostly with three leaves at the same node. It is not rare to find that in the transition from the hypotagma to the main florescence the position of the leaves changes from decussate to alternate (e.g., *Epilobium montanum* L.).

The subtending leaves of the flowers can be quite different within the same genus. They can be bracteose as in *Fuchsia arborescens* Sims (Fig. 15 II) or foliaceous as in *Fuchsia magellanica* Lam. (Fig. 14), giving the inflorescence a "naked" or "leafy" shape. In many species of *Epilobium* or, for example, in *Oenothera biennis* (Fig. 4), they are leafy in the basal part of the florescences, diminishing distally, and finally becoming bracteose (frondo-bracteose foliation). Only in *Circaea* are the subtending leaves of the flowers missing. With the exception of the genus *Ludwigia*, the flowers do not bear prophylls.

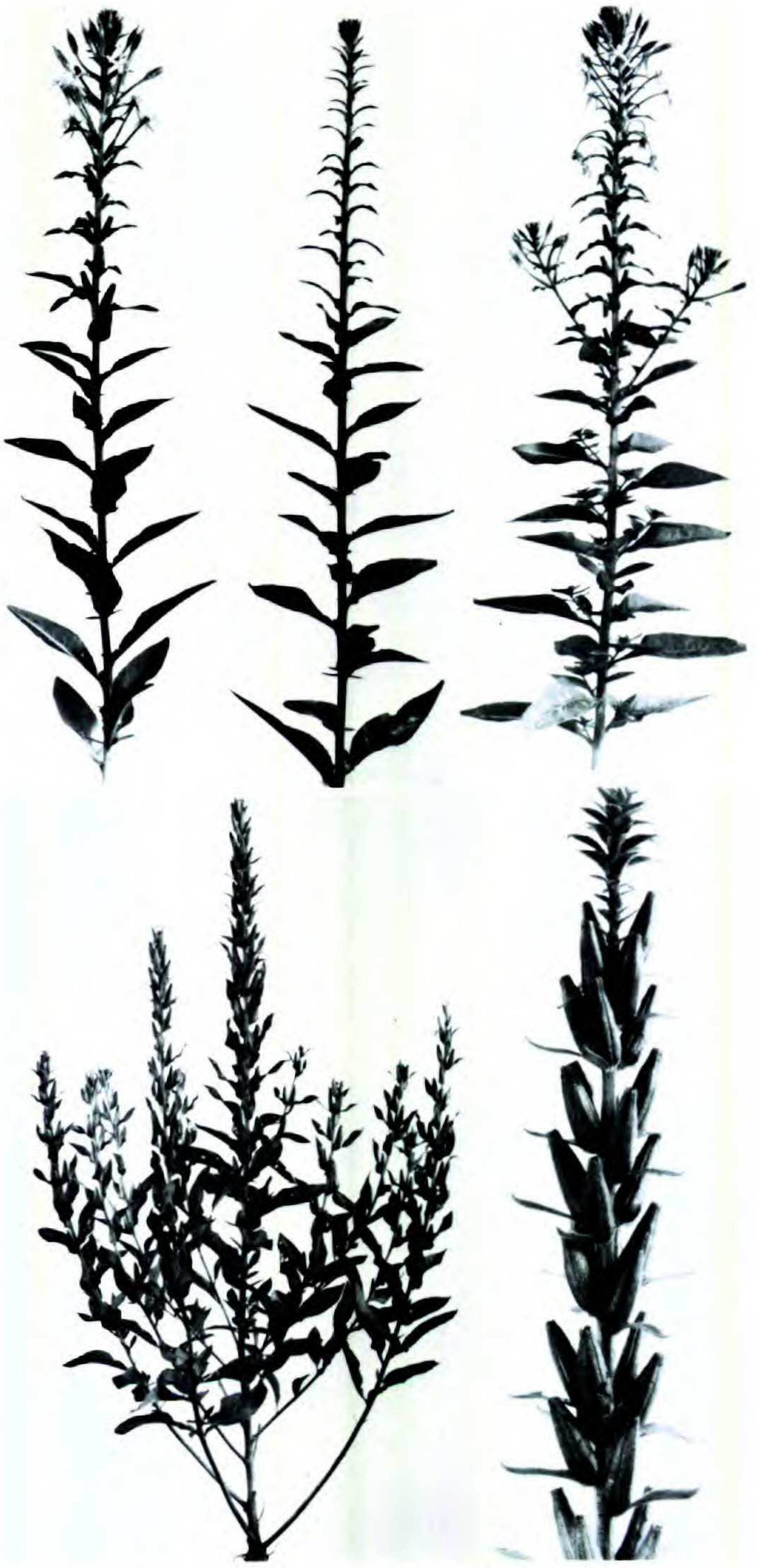

FIGURE 4. *Onagraceae.* Oenothera biennis.—*Top, left. Flowering plant.—Top, center. The same plant with the flowers cut off to show the frondo-bracteose foliation.—Top, right. With developing paracladia.—Bottom, left. Plant with fully developed paracladia zone.—Bottom, right. Proliferation apex of the main florescence. (Original photographs from Troll.)*

Many representatives of the family are half-rosette plants, which means that the primary